Agonistic interactions in female New Zealand fur seals:

the functions of conspecific aggression and its implications in spatial population dynamics

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I would like to dedicate this research to Mother Nature, who is being purged of her children, along with all the good things that allow the existence of countless life forms.

Table of Contents

Table of Figures

List of Tables

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Abstract

Female conspecific aggression is widespread in the order Pinnipedia, which include phocids (true seals), otariids (fur seals and sea lions) and odobenid (walruses). Although the functions of female aggression have been explored in a number of pinniped species, the proposed functions vary greatly between species. The aim of this research was to investigate the functions of female aggression in the New Zealand fur seal (*Arctocephalus forsteri*), and to assess the vast differences in the social interactions and reproductive ecology that may explain the disparity between species. As a common social behaviour, aggression between the individuals of a group and the resulting competition for resources can have a considerable influence on the spatial population dynamics by regulating the degree of emigration and immigration. Therefore, this research also explored the effects of female aggression of the New Zealand fur seal on the dispersion of females within the rookery to quantify its effects on the spatial population dynamics, and to estimate the carrying capacity of the rookery area studied.

This study focused on a subset population of the Ohau Point seal colony, north of Kaikoura, New Zealand. A non-invasive method was used to make 184 observations of unmarked focal females over the 2014 – 2015 breeding season and the first three months of the pup rearing season. This research employed methods of quantifying aggression, such as aggression distance and the proportion of aggression, which were not commonly used in past studies of pinniped behaviour, to study its effects on the spatial population dynamics. Conspecific aggression in females was found to be prevalent in this species; however, the rate of inter-female aggression was significantly lower than other species of otariids. The results of this study showed that thermoregulation, offspring defence and resource defence were the primary functions of aggression in this species, although female aggression was found to have no influence on the dispersion of females, and subsequently, the spatial population dynamics of this species. Therefore, the nearest-neighbour distance was employed to measure the degree of female dispersion, and to predict the carrying capacity of the study area. In analysing the result of this prediction, a conclusion was reached that the nearest-neighbour distance was insufficient to represent the dispersion of females of the

terrestrially-breeding colonial mammal, due to its minimal inclusion of space required between resting females for movement. This led to the proposal of a new method of measuring the individual dispersion in this species using the distance from all direct neighbours of the focal animal, and a recommendation for further research.

Introduction

Coloniality and spatial population dynamics

Coloniality is commonly found in many terrestrial birds, reptiles, marine mammals and most seabirds (Lack 1968; Trillmich & Trillmich 1984; Anderson & Hodum 1993; Danchin & Wagner 1997; Neff, Cargnelli & Côté 2004). The definition of colonial breeding is "a form of group living in which individuals breed within densely distributed nesting territories that contain no resources other than nesting sites"(Perrins & Birkhead 1983). As coloniality can accrue significant individual reproductive costs, its occurrence had been regarded as inexplicable by some from an evolutionary perspective (e.g., Danchin & Wagner 1997). Costs that arise from group-breeding include increased competition for resources such as space, food and mates, increased disease and parasite transmission, nest parasitism, conspecific aggression and infanticide, which may contribute to a reduction in the reproductive output of a population (Danchin & Wagner 1997; Davis & Brown 1999; Hötker 2000; Ashbrook *et al.* 2008; Breed, Don Bowen & Leonard 2013). However, the high frequency of coloniality across multiple taxa suggests that coloniality must also provide benefits (Danchin & Wagner 1997). Depending on the species, the benefits of colonial breeding may be reduced predation, shared efforts to protect offspring, increased likelihood of finding mates and access to information such as the location of food resources (Brown & Orians 1970; Burger 1988; Becker 1995; Ashbrook *et al.* 2008). For example, common tern nests with shorter nearest-neighbour distance were found to have higher reproductive success than nests with longer nearest-neighbour distance, as nests in denser colonies were better protected against predation (Becker 1995). Most of the proposed costs and benefits of group-breeding have originated from work on seabirds, due to the significantly high occurrence of coloniality (98% of seabirds) (Lack 1968).

In many colonial species, the primary factor that regulates breeder population growth is the availability and use of space which significantly impact the reproductive decisions of individuals (Hötker 2000; Nevoux *et al.* 2010). Therefore, coloniality has also been proposed to have arisen in some species from a lack of suitable breeding habitat, such as in the avocet (*Recurvirostra avosetta*) (Hötker 2000) and purple martin (*Progne subis*)

(Davis & Brown 1999). In pinnipeds and seabirds, terrestrial space is the primary feature of the breeding habitat which limits the reproductive output of a colony, as breeding and care for the young occur on land while nutrition is acquired from the ocean (Bartholomew 1970; Gentry 1973; Cassini 2000). When there is a lack of available breeding space, individuals, especially new breeders can either be prevented from reproducing or forced to disperse to find this resource which may result in a decrease in the net productivity of the population or the formation of new colonies (Brown & Orians 1970; Kokko & Sutherland 1998; Bradshaw, Lalas & Thompson 2000). Both of these assert density-dependent limitations on the number of individuals able to reproduce in the colony (Hötker 2000), and may facilitate emigration (Armitage 1991; Bocedi *et al.* 2014). Therefore, the space requirements of individuals that arise from social behaviour inevitably have a great influence on spatial population dynamics (Kokko & Sutherland 1998). In addition, the dispersal of individuals mediated by individual spatial requirements is an important driving force behind population range expansion, and is crucial in understanding the population dynamics in invasive, threatened or recolonising populations (Bocedi *et al.* 2014; Bateman *et al.* 2015).

Some colonially breeding species show preference for certain habitat features, which can significantly influence the distribution (geographical location of animals) and dispersion (the degree of physical separation between animals) of individuals in an area, and therefore mediate the carrying capacity of the breeding site and population dynamics (Kokko & Sutherland 1998; Kokko, Harris & Wanless 2004; López-Sepulcre & Kokko 2005; Balbontín & Ferrer 2008; Nevoux *et al.* 2010). Site-dependent habitat selection is thought to maximize the individual reproductive fitness by preferential occupancy of high quality sites in heterogeneous habitats (Krüger & Lindström 2001; Parker *et al.* 2008); this may result in ideal-free distributions, which occur when individuals are distributed in accordance to the perceived quality of the habitat (Danchin & Wagner 1997). The perceived quality of a site can be inferred from its occupancy, comparison of the reproductive success of the occupants to conspecifics in other sites, or by observing the successive order of site occupancy (Krüger & Lindström 2001; Kokko *et al.* 2004; Matthiopoulos, Harwood & Thomas 2005; Balbontín & Ferrer 2008). For example, due to the higher reproductive success of island-nesting avocets

and earlier occupancy of island nesting sites in comparison to the mainland, islands were suggested to be of higher quality habitats for breeding avocets (Hötker 2000). Furthermore, Goshawk *(Accipiter gentilis*) nests which were taken earlier were found to have higher reproductive success (Krüger & Lindström 2001). Habitats that are highly heterogeneous result in increased competition for high quality sites and more individuals occupying low quality sites, leading to a reduction in the *per capita* reproductive success (Krüger & Lindström 2001; Nevoux *et al.* 2010).

Social behaviour in colonies

The social behaviour in group-living species can significantly influence population dynamics, through the regulation of population size and facilitation of inter-population interactions (Tamarin 1983; Armitage 1991). Conspecific aggression, one of the main social behaviours, is the most commonly used to regulate space use by individuals (McBride 1971). Agonistic behaviour between conspecifics is commonly seen in 'distance' species, where individuals have a threshold distance at which aggression is displayed to an approaching individual, as opposed to 'contact' species, which tolerate or seek physical contact with one another (Brown & Orians 1970; Grubb 1974). In colonially breeding species such as seabirds, conspecific aggression can influence the degree of dispersion between reproductive individuals through the formation of territories (Brown & Orians 1970; Bowers & Matter 1997), where a territory is defined as an area around an individual that is defended from conspecifics (Noble 1939), and has been suggested to be a significant population limiting factor, especially in birds (Newton 1992). Since aggressive behaviour is the primary behaviour used in defence, territory size may be inferred from measurements of approach-tolerance distance; the distance at which displays of aggression occur between conspecifics (Conder 1949). Territoriality significantly reduces the carrying capacity of a given area, as aggression can prevent conspecifics from establishing and reproducing nearby (Hötker 2000; Miller *et al.* 2014). For example, increasing density was seen to increase the incidence of clutch abandonment in avocet colonies (Hötker 2000). Thus far, a large proportion of past studies of territoriality and individual distance in colonial species have focused primarily on seabirds and terrestrial birds (e.g., Lill 1968; Grubb 1974; Beal 1978), along with a few on non-colonially breeding species (e.g., Hermit crabs Clibanarius spp.:

Hazlett 1975). Therefore, research on the social behaviour of mammalian colonial species would be valuable in further understanding of the mechanisms of population dynamics. In particular, there is a lack of research on the dynamics of population expansion in pinnipeds, and how it is influenced by inter-individual interactions. My research aims to fill this gap by analysing the inter-individual interactions and investigating how these influence the individual space requirements. I expect the knowledge gained from this study will be of significant assistance in the development of management plans for the rapidly growing New Zealand fur seal population, especially when coupled with deeper understanding of the mechanisms of breeding habitat selection and the assessment of potential breeding habitats around the New Zealand coastline.

Coloniality in Pinnipeds

As the mammalian taxa with the most extreme polygynous mating system, pinnipeds are regarded as the ideal group in which to study the benefits and costs of group-breeding (Francis 1987; Carey 1989; Cappozzo, Túnez & Cassini 2008). Most pinniped species aggregate in large numbers to form breeding colonies every year during their summer breeding seasons (Miller 1975; Francis 1987; Wickens & York 1997). Large colonies of pinnipeds are thought to be formed through philopatry in most species, resulting in many generations returning to their birth site through the entirety of their lifespan (Bradshaw *et al.* 2000; Parker *et al.* 2008). Within the congregation, the females of some pinniped species, such as the elephant seals (*Mirounga spp.*) and the sea lions (subfamily Otariinae), form sub-groups, while others, such as fur seals, individually space themselves out, usually about one body length from others (New Zealand fur seals, Gentry 1973; Gentry 1987; Carey 1991; Northern elephant seals, Baldi *et al.* 1996; South American sea lions, Cappozzo *et al.* 2008).

Due to the highly polygynous mating system of pinnipeds, the benefits of colonial breeding to breeding males is significant and easily identified as increased reproductive success (Bartholomew 1970; Carey 1991), while the benefit to females is less clear (Carey 1992). Grouping in large numbers has been proposed to provide a number of benefits to female pinnipeds, either directly to them, or indirectly via their offspring

(Campagna *et al.* 1992; Cassini 2000). Group-breeding in females may have evolved to increase inter-male competition as males compete with one another to gain access to the females, allowing the females to identify and select the fittest males with whom to copulate; which in turn increases their reproductive fitness (McLaren 1967; Bartholomew 1970). Male competition also helps females avoid harassment from subordinate males, as the dominant males aggressively protect their harem of females or their territory in which females are established, through the exclusion of sub-dominant males from their territories (Doidge, Croxall & Baker 1984; Carey 1989; Francis & Boness 1991; Cassini 1999).

In otariids it has been suggested that females group together to reduce their individual rate of interaction with males (Campagna *et al.* 1992; Cassini 2000; Cassini & Fernández-Juricic 2003). For example, Cappozzo *et al.* (2008) found that female South American sea lions (*Otaria flavescens*) in larger breeding groups experience lower rates of individual interaction with males due to a 'dilution effect', where each female experiences less encounters with the dominant male as a result of the higher number of females (Cappozzo *et al.* 2008). The avoidance of males observed in females of many pinniped species are suggested to stem from the high level of physical harm that males can inflict on females, due to the extreme sexual dimorphism in body size in most species of the families otariidae and in some phocidae (Miller 1975; Reiter, Panken & Le Boeuf 1981; Trillmich & Trillmich 1984; Campagna *et al.* 1992; Le Boeuf & Campagna 1994; Bohórquez-Herrera *et al.* 2014). The sexual dimorphism may be as extreme as the body mass of a male being seven times the mass of a female in some species (Wickens & York 1997). In the New Zealand fur seals, males can weigh more than three times the size of females during the breeding season, as they increase their neck girthand gain body weight for inter-male competition (Crawley & Wilson 1976; Carey 1991; Goldsworthy & Gales 2008). Campagna, Le Boeuf and Cappozzo (1988) proposed that tight grouping in female southern sea lions (*Otaria byronia*) may be due to the risk of adult female mortality from female-raiding behaviour by satellite males, where sub-dominant males carry off females in their mouths from within the territory of dominant males. This behaviour has also been observed to cause pup mortality, as sub-dominant males also abducted pups (Campagna *et al.* 1988). A study comparing the colony breeding southern sea lions and solitary breeding sea lions found that group-breeding

females experienced a reduced rate of harassment by sub-dominant males, positively influencing the survival rate of both females and pups (Campagna *et al.* 1992). However, pup defence may not be the primary cause of female avoidance of males in species such as the fur seals, in which females do not experience mortality from male interaction, as female aggression toward males have been observed even in the absence of a pup (Harcourt 1992b).

Aggregation can also incur costs to female pinnipeds due to density-dependent mechanisms (Francis 1987; Cassini 2000). Increase in female density usually results in increased inter-female competition for resources such as suitable substrates for birthing, resting and thermoregulation (Reiter *et al.* 1981; Maestripieri 1992; Cassini 2001; Cassini & Fernández-Juricic 2003; Fernández-Juricic & Cassini 2007). Increased competition and the saturation of individuals on high quality substrates may lead to a greater thermal stress in females, due to the requirements of higher frequency of territory defence or visits to thermoregulatory resources such as the sea, pools or shade. Colony density has also been found to positively correlate to pup mortality, primarily caused through intensified conspecific aggression and starvation (Doidge *et al.* 1984; Cassini 2000, 2001; Lourie, Hoskins & Arnould 2014), as adult female pinnipeds commonly display a strong aggression towards non-filial pups (Harcourt 1992a; Maestripieri 1992; Cassini & Fernández-Juricic 2003). In many pinniped species, such female-pup aggression can result in the pup sustaining fatal injuries, for example, due to bites to the head (Harcourt 1992a; Le Boeuf & Campagna 1994). Density-related juvenile mortality has also been explored in other colonially breeding species, such as seabirds. The Great black-backed gull (*Larus marinus*) chicks of high density colonies were less likely to survive than chicks of low density colonies, due to the higher likelihood of conspecific aggression (Butler & Trivelpiece 1981). In pinnipeds, mother-pup separation is suggested to occur more frequently in high-density congregations, also due to the increased level of inter-female aggression (Francis 1987; Harcourt 1992a; Cassini & Fernández-Juricic 2003). Separations in high density colonies are likely to be followed by greater difficulties in locating each other through vocal recognition due to the amplified background noise, which can lead to prolonged periods of pup starvation (Boness *et al.* 1992; Charrier, Mathevon & Jouventin 2003). Therefore, female aggression, which can be seen in a number of pinnipeds, has been suggested as

the primary method evolved to counter the detrimental effects of aggregation such as these.

Conspecific female aggression and territoriality

Conspecific aggression is most commonly found in the males of polygynous species, as they compete to acquire and defend their access to females to increase their reproductive success (Christenson & Le Boeuf 1978; Armitage 1991; Bohórquez-Herrera *et al.* 2014). Conspecific aggression in females is usually of lower intensity (Floody & Pfaff 1977), and has not been as extensively studied as inter-male aggression (Clutton-Brock 2009). Female conspecific aggression in animals is most commonly seen in the form of food resource defence (Armitage 1991; Wolff & Peterson 1998; Huchard & Cowlishaw 2011) or maternal aggression, which functions to defend offspring against conspecific infanticide (Wolff 1985; Maestripieri 1992). Conspecific aggression in group-breeding animals can result in a partitioning of breeding spaces, which each individual actively defends from one another (Brown & Orians 1970). These 'territories' usually allow individuals to gain exclusive access and monopolize the resources within the area, which are necessary for survival and/or reproductive success; these may include food, mates or shelter from predation or the environment (Caron & Beaugrand 1988; Genner, Turner & Hawkins 1999; López-Sepulcre & Kokko 2005). Since high level of aggression in conspecifics is indicative of increased competition, which generally results from increased density (Maestripieri 1992; Cassini 2001; Fernández-Juricic & Cassini 2007), aggression is able to prompt emigration and prevent immigration (Young, González-Suárez & Gerber 2008). For example, Christenson and Le Boeuf (1978) found that the movement of pregnant female Northern elephant seals between beaches was caused by inter-female aggression. As conspecific aggression has direct effects on the population size in colonial species through the formation and maintenance of territories, it is expected to assert a significant influence on species survival and population dynamics (Brown & Orians 1970; Svare 1990).

Conspecific aggression in pinnipeds

The females of many pinniped species display agonistic behaviour towards other females of conspecifics during their resting and breeding periods on land (Carey 1992; Le Boeuf & Campagna 1994; Neumann 1999; Cassini 2000; Fernández-Juricic & Cassini 2007; Young *et al.* 2008). A variety of hypotheses have been suggested to explain the intra-sexual aggression in female pinnipeds, such as changes in hormonal levels during breeding (Atkinson 1997; as cited in Maniscalco *et al.* 2007), rousing of male competition (Cox & Le Boeuf 1977), pup protection, territory defence and thermoregulation (Carey 1992; Le Boeuf & Campagna 1994; Cassini 2000; Fernández-Juricic & Cassini 2007). Female aggression has also been attributed to food resource defence in most mammalian species, due to its significant contribution to their reproductive success (Sterck & Steenbeek 1997; Wolff & Peterson 1998; Huchard & Cowlishaw 2011; Miller *et al.* 2014); however, this does not seem applicable to pinnipeds which only utilize terrestrial habitats for breeding and resting and obtain nutrition only from the ocean (i.e. food defence would not be applicable to above-land conspecific aggression in pinnipeds) (Carey 1991; Francis & Boness 1991; Lento *et al.* 1997; Cassini 2000).

Many mammalian females exhibit increased levels of aggression during reproductive periods, which in some species, is primarily attributed to increased hormone levels (Floody & Pfaff 1977; Svare 1990). For example, mice (*Mus domesticus*) display aggression towards conspecific males during pregnancy and after parturition (Svare 1990). Increased aggression during and immediately after birth may significantly increase the survival probability of offspring, as offspring are the most vulnerable early in their lives (Maestripieri 1992). For example, Doidge *et al.* (1984) found that in the Antarctic fur seal (*Arctocephalus gazella*), half of the total pup mortality before weaning is accounted by deaths that occurred within the first two days of birth. Conspecific aggression has also been found to occur without influence from reproductive hormones, as illustrated in a study of prairie voles (*Microtus ochrogaster*) which showed inter-female aggression following a period of co-habituation with a male, even without the occurrence of mating (Bowler, Cushing & Carter 2002). Pinniped species have not been observed to display conspecific aggression exclusively during the reproductive period,

suggesting that there are factors other than hormone cycles inducing the conspecific aggression behaviour.

Female aggression has been proposed as a behaviour that serves to increase the reproductive fitness of females by inducing inter-male aggression and attracting males via monopolisation of the males 'peace-keeping' behaviour (Miller 1974; Cox & Le Boeuf 1977; Maestripieri 1992). In many colonially breeding pinnipeds where territorial males defend a group of females or a breeding space, males show a tendency to interrupt agonistic interactions between the females or investigate female aggression towards other males, within or nearby his group or territory (Miller 1974; Cox & Le Boeuf 1977; Harcourt 1991). Such behaviour may lead to aggressive encounters with neighbouring males, the result of which could influence the females' mate choice (Maestripieri 1992). This method of assessing the male fitness would benefit the reproductive fitness of the females as they preferentially mate with the older and dominant male, thereby producing offspring that may subsequently experience increased rate of survival (Cox & Le Boeuf 1977).

Pup protection has also been suggested as a primary reason for inter-female aggression in pinnipeds, as females often threaten and attack unrelated pups (Boness, Anderson & Cox 1982; Harcourt 1992b; Wolff & Peterson 1998; Cassini 2001; Fernández-Juricic & Cassini 2007). It has been suggested that female aggression protects offspring by forming a defensive barrier around the female and her offspring (Cassini 2001). Female aggression as a function of offspring defence from both predators and conspecifics is found in numerous mammalian and avian species (Andersson, Wiklund & Rundgren 1980; Wolff & Peterson 1998). For example, both Harcourt (1992b) and Cassini (2001) found that females without suckling offspring were significantly less aggressive towards other females than females with suckling offspring in Peruvian and Uruguayan colonies of the South American fur seal (*Arctocephalus australis*). Increased female aggression following parturition may reduce potential attacks towards offspring from other females, safeguarding the female's reproductive fitness by increasing the probability of offspring survival (Boness *et al.* 1982; Maestripieri 1992; Cassini 2001). For example, female Northern elephant seals (*Mirounga angustirostris*) that initiated more aggressive interactions were more likely to successfully rear their pups to weaning (Christenson & Le Boeuf 1978). Harcourt (1992b) also found that female aggression was pronounced

during the perinatal period. Another study on the grey seals (*Halichoerus grypus*) found that the likelihood of inter-female aggression depended on the location of the aggressor's offspring and that females displayed lower levels of aggression in the second half of lactation (Boness *et al.* 1982). Such findings support the hypothesis of female aggression as the primary function of offspring defence as new-borns are more vulnerable to conspecific attacks than older animals, requiring more maternal protection (Harcourt 1992b; Maestripieri 1992; Le Boeuf & Campagna 1994). In a number of otariid species, starvation and death caused by attacks from conspecifics are the highest rated causes of pup mortality (Mattlin 1978b; Harcourt 1991, 1992a; Cassini & Fernández-Juricic 2003). Offspring mortality caused by female colony-mates has also been observed in at least one seabird, such as the common guillemot (*Uria aalge*) (Ashbrook *et al.* 2008). However, offspring defence alone cannot explain the existence of inter-female aggression in New Zealand fur seals or other pinnipeds, as this behaviour is commonly observed even in non-lactating females and females whose pups are absent from the female's vicinity (Francis 1987; Maestripieri 1992).

Finally, behavioural thermoregulation and competition for space have also been proposed as the purpose for female aggression in many otariid species as well as in a number of phocids (Carey 1992; Neumann 1999; Cassini 2001; Young *et al.* 2008). Fur seals have dense, highly insulating fur to aid them in deep-water foraging; however, this often results in overheating on land (Limberger *et al.* 1986; Campagna & Le Boeuf 1988). The contrasting intensities of gregariousness between the fur seals and sea lions can support the theory of thermoregulation as a function of aggression, as fur seals have much more potential to retain heat in comparison to the sea lions which are more tolerant of body contact (Gentry 1973; Trillmich & Trillmich 1984; Carey 1991; Cassini 2000). The frequency and strength of agonistic interactions has also been found to be dependent on the location within the rookery in some otariid species, as their range of thermoregulatory behaviours include preferences for resting and breeding sites with specific features (Carey 1989, 1992; Cassini 2000; Bohórquez-Herrera *et al.* 2014; Lourie *et al.* 2014). For example, a study on Californian sea lions (*Zalophus californianus*) by Bohórquez-Herrera *et al.* (2014) has shown that sites which provide mechanisms for thermoregulation such as pools and shade are preferred for breeding and resting, resulting in agonistic interactions being concentrated around these areas. Carey (1992)

found that there was a higher likelihood of agonistic encounters between female New Zealand fur seals around cooling substrates such as pools and shade compared to substrates exposed to the sun. The defence of preferred microhabitat as the female's 'territory' would allow the defending female to utilise the cooling resources constantly, without needing to travel through the colony to find thermoregulatory substrate elsewhere (Carey 1992). Inter-female aggression has also been observed in some phocids such as the northern elephant seals and harbour seals (*Phoca vitulina*), with the functions of aggression suggested as space defence for pup protection and space defence in limited haul out locations, respectively (Northern elephant seal, Christenson & Le Boeuf 1978; Harbour seal, Neumann 1999).

As outlined above, numerous past studies have analysed the female conspecific aggression across the Pinnipedia; however, the results and discussions of these studies concentrate on the functions of aggression, and not the influence of this social behaviour on the population dynamics (Boness *et al.* 1982; Carey 1992; Neumann 1999; Cassini 2001; Fernández-Juricic & Cassini 2007). My research aims to fill this gap by utilizing the ideas and methodologies previously used primarily in the studies of colonial bird populations to investigate the effects of conspecific aggression on the rookery population processes of a pinniped species, the New Zealand fur seal.

Fur seals

Fur seals and sea lions (Otariidae) constitute one of three families of order Pinnipedia, along with true seals (Phocidae) and walruses (Odobenidae) (Wickens & York 1997). Nine species of fur seals occupy colonies worldwide, the largest population at 1.5 million individuals (Cape fur seal, *Arctocephalus pusillus pusillus*) and the smallest at 7,000 individuals (Guadalupe fur seal, *Arctocephalus townsendi*) (Trillmich 1990; Wickens & York 1997). Most fur seal species are under legal protection, although none of them are considered to be in decline (Wickens & York 1997). All species of the family Otariidae breed in colonies, and display a strong polygynous mating system, where dominant males defend a group of females or a territory containing females against other males for exclusive access (Nutting 1891; Carey 1989; Campagna *et al.* 1992). Fur seals usually give birth to only one offspring and rear a single young annually, apart

from the Galapagos fur seal (*Arctocephalus galapagoensis*) in which some females may continue to nurse their yearlings after giving birth to a new-born (Wickens & York 1997; Trillmich & Wolf 2008). All fur seal species are income breeders that forage in between nursing their young, as opposed to capital breeding, which is characteristic of most phocids that nurse their young from stored reserves until weaning (Boness & Bowen 1996; Bowen *et al.* 2006; McDonald *et al.* 2012; Breed *et al.* 2013). Six of the fur seal species reside in the southern hemisphere, one of them being the New Zealand fur seal (Wickens & York 1997; Garlepp, Logan & Kirkwood 2013).

New Zealand fur seals

New Zealand fur seals are one of the two native pinniped species of New Zealand, alongside the New Zealand (or Hooker's) sea lion (*Phocartos hookeri*) (Crawley & Wilson 1976). They are a protected species, under the New Zealand Marine Mammals Protection Act of 1978 (Cawthorn 1985; Lalas & Bradshaw 2001). New Zealand fur seals are distributed around the coastlines of New Zealand mainland, offshore islands, Southern Australia and the sub-Antarctic islands (King 1969; Crawley & Wilson 1976; Harcourt 2001). The current population size of the New Zealand fur seals in New Zealand is unknown; however, a New Zealand population estimation of up to 100,000 seals was suggested in 2001 (Harcourt 2001) and an Australian population estimation of approximately 40,000 in 2003 (Goldsworthy *et al.* 2003).

New Zealand fur seals, along with most other species of fur seals, congregate annually in high numbers on rocky coastlines to mate, give birth and raise offspring (Crawley & Wilson 1976; Goldsworthy & Shaughnessy 1994; Bradshaw *et al.* 1999). However, unlike many true seals (Phocidae) and sea lions, females of New Zealand fur seals display a highly anti-gregarious behaviour in the form of aggression towards conspecifics during the rearing period, as do most species of fur seal (Carey 1991, 1992; Harcourt 1992b; Cassini 2000, 2001). Males reach sexual maturity around 5-6 years of age, but do not grow big enough to hold breeding territories until approximately 8-9 years of age (Dickie & Dawson 2003). Females reach sexual maturity around 4-6 years of age (Dickie & Dawson 2003) and both sexes are known to live to around 14-15 years (Mattlin 1978a).

The large males start to arrive at rookeries from early October to obtain territories, which they attempt to maintain for the duration of the breeding season to gain exclusive access to the females within their territories, known as 'resource-defence polygyny' (Carey 1992; Goldsworthy & Shaughnessy 1994). To protect their territories and mating opportunities, males remain highly vigilant for any other males entering their territories and violent fights between large, dominant males are frequent during the period of peak density (Carey 1991). Subordinate males are frequently observed attempting to enter rookeries for mating opportunities, and while some successfully mate, they usually are quickly driven away by the large dominant males (Goldsworthy & Shaughnessy 1994; Wickens & York 1997). Females pregnant from the last breeding season begin to arrive from late October to December to give birth, and the peak birthing period is December to January, and mating occurs about 7-8 days postpartum (Stirling 1971; Miller 1975; Carey 1992; Goldsworthy & Shaughnessy 1994). New Zealand fur seals usually give birth to a single pup as with most pinnipeds (Bester & Bartlett 1990; Wickens & York 1997), and females alternate between nursing periods on land and feeding trips at sea to continually feed and care for their pups over a 9-10 month period, after which the pups are weaned (McNab & Crawley 1975; Miller 1975).

Conflicts between humans and seals

Since the banning of the commercial harvesting of seals by the Europeans in the 1980s, which almost drove them to extinction, rapid growth in the population size of New Zealand fur seals in New Zealand and Australia have been observed (Ryan, Hickling & Wilson 1997; Bradshaw *et al.* 2000; Boren, Muller & Gemmell 2006). The New Zealand fur seal population has been steadily increasing since its protection in 1875, following a near-extinction event in 1800-1900s due to commercial harvesting (Crawley & Wilson 1976; Dix 1993; Ryan *et al.* 1997; Lalas & Bradshaw 2001; Boren *et al.* 2006). As the population expands, human and fur seal conflicts can be expected to increase in response (Lalas & Bradshaw 2001; Boren 2010), and the increased rate of encounter between these two species may become highly problematic in a number of sectors, such as the commercial fisheries and ecotourism (Barton *et al.* 1998; Bradshaw *et al.* 1999; Lalas & Bradshaw 2001; Boren, Gemmell & Barton 2002; Higham & Shelton 2011). As they re-colonise their former breeding grounds, there has already been concerns over

potential conflicts between the fur seals and humans (Taylor *et al.* 1995; Wickens & York 1997; Lalas & Bradshaw 2001; Boren 2010). The commercial fisheries and public fishermen are likely to increasingly perceive fur seals as serious competitors for fishing stock, resulting in potential mass culling and retaliatory killing of the seals (Boren 2010; Butler *et al.* 2011; Schakner & Blumstein 2013). Seals are also blamed for damaging fishing gear and deaths of seals may occur from interactions with equipment such as trawl nets (Lalas & Bradshaw 2001; Yodzis 2001; Schakner & Blumstein 2013; Cronin *et al.* 2014). There already have been numerous examples of conflict occurrence between seals and fisheries in other species of seals, especially with increases in seal populations occurring in conjunction with decreasing fish stocks (Butler *et al.* 2011; Cronin *et al.* 2014). Many pinniped species that inhabit waters near large human settlements are likely to be implicated in some sort of conflict with commercial or recreational fishermen, and thus are regarded as a serious concern due to the decline in commercial fish stocks around the world (Augé, Moore & Chilvers 2012; Cronin, Gerritsen & Reid 2012; Cronin *et al.* 2014). There are two main types of conflicts that occur between the seals and fisheries; operational interaction and biological interaction. Operational interaction refers to instances of seals directly taking fish already caught in fishing equipment, cause equipment damage and entanglements of seals in equipment. In a salmon trap-net fishery (*Salmo salar*) in the Gulf of Bothnia, seals reportedly damage over 50% of the catch, which is a considerable loss (Suuronen *et al.* 2006). By attacking fish caught in a trap-net, seals can also cause damage to the fishing equipment, incurring further expenses to the fishermen (Kauppinen, Siira & Suuronen 2005). Biological interaction refers to both direct competition for the same prey species and indirect competition through the marine food web (Lalas & Bradshaw 2001; Kemper *et al.* 2003; Cronin *et al.* 2012; Cronin *et al.* 2014). Many populations of seals target commercially fished species, such as salmon, whitefish (*Coregonus spp.*), herring (*Clupea harengus*), cod (*Gadus spp.*), flounder (*Platychtys flesus*), arrow squid (*Nototodaus sloanii*), hoki and mackerel (*Trachurus spp.*) (Lalas & Bradshaw 2001; Lundström *et al.* 2007; Chilvers 2008; Boren 2010; Butler *et al.* 2011). However, there has been no evidence of significant detrimental influence to fisheries arising from direct competition with the seals (Trites, Christensen & Pauly 1997; Houle *et al.* 2016).

There are a number of cases where an increase in pinniped population resulted in higher rate of conflict between fisheries and the seals. For example, a local increase in grey seal populations in the Clyde sea, Scotland, has led to increased perception among fishermen that grey seals are a significant threat to their livelihoods (Moore 2003). Also, the recent increase in harbour and grey seal populations in Europe resulted in an increased rate of conflict with Scottish salmon fisheries, resulting in a development of a management plan to minimize human-seal conflict (Butler *et al.* 2011). The rapid increase of the grey seal population of the Baltic Sea caused an increase in fisheries and seal conflict in numerous countries, and it is estimated that the coastal fisheries are experiencing considerable losses from depredation of fish from nets and gear damage; this has resulted in the government of Finland allowing limited culls and hunting of this species (Varjopuro 2011). Since the population increase, the perceived negative impacts of the grey and harbour seal species on the fisheries in Ireland has led to a frequent demand for culls (Cronin *et al.* 2014).

Pinnipeds, and particularly otariids, are the marine mammals that are the most likely to be implicated in negative interactions with marine aquaculture industries (Kemper *et al.* 2003). Many species of seals hold a negative reputation for targeting commercial fish species in aquaculture pens, with the conflicts between aquaculture farms and seals predicted to continue as studies on effective seal repellent and exclusion methods are ongoing (Kemper *et al.* 2003; Robinson *et al.* 2008). Aquaculture industries are growing in importance, as the wild commercial fish stocks continue to decline (Pauly *et al.* 2002). Finfish aquaculture industries, such as salmon farms are the most frequently targeted by otariids around the world, and experience damages worth millions of dollars (Kemper *et al.* 2003). Approximately 2 to 10 million dollars of the gross production is thought to be lost to depredation by marine mammals (Nash, Iwamoto & Mahnken 2000). Before the industry expansion in the 1990s, it was found that marine aquaculture (mariculture) farms closer to a large seal haul out location had increasingly significant vulnerability to more frequent attacks from seals (Kemper *et al.* 2003). Although New Zealand fur seals are not the only marine mammals to cause damage to commercial fisheries and aquaculture equipment and stock (Schakner & Blumstein 2013), they may attract disproportionately significant negative attention due to their rapidly increasing population (Bradshaw *et al.* 2000).

Seal interactions with humans or man-made items can inevitably be detrimental to seals as well. Entanglement in fishing gear is also fatal for many seals, and seal bycatch by fishing vessels is showing an increasing trend (Cawthorn & Wells 2008; as cited in Boren 2010; Augé *et al.* 2012). Both offshore fisheries and finfish mariculturalists of New Zealand are frequently implicated in conflicts with New Zealand fur seals. Trawl net fisheries experience a high frequency of seal conflicts, as seals targeting the fish in trawl nets are easily trapped and drowned (Lalas & Bradshaw 2001). Estimates of 456 to 1426 fur seal drowning s in trawl nets in the New Zealand Exclusive Economic Zone from 1990 to 1993 has been suggested (Gibson 1995, as cited in Lalas & Bradshaw 2001). Additionally, the incidence of fatality in relation to the bycatch by squid trawl nets in the New Zealand sea lions is proposed to be the primary threat to the small population of this rare species (Chilvers 2008). Due to the threatened state of the New Zealand sea lions, efforts to minimize accidental kills are include a limit on the number of kills by the squid fishery, and the production of a sea lion exclusion device (SLED) (Chilvers 2008). In contrast, the primary focus of fur seal exclusion and repellent methods usually is to minimize the damage to gear and catch, as many species of fur seals are rapidly increasing (e.g., Suuronen *et al.* 2006). The damage on the mariculture industry caused by New Zealand fur seals was estimated to be NZ $2 million per annum as of 2003 (Kemper *et al.* 2003). New Zealand fur seals, along with all other species of seals, in the 200 nautical mile Exclusive Economic Zone are protected under the Marine Mammal Protection Act 1978, prohibiting all killing and harassing of pinnipeds (Lalas & Bradshaw 2001). Despite this, there have been instances of illegal culling of seals by shooting (Kemper *et al.* 2003). Relocation or culling of seals that repeatedly target farmed stock are also practiced by a number of marine farms to minimize stock loss (Kemper *et al.* 2003; Robinson *et al.* 2008; Butler *et al.* 2011), which would be definitively (in case of cull) or potentially (in case of relocation) detrimental to the animal. By having a negative impact on the survival rate, such control measures may significantly reduce the population persistence, especially if the population is small and declining.

Further conflict may arise between humans and seals over the usage of coastal space. As the growing fur seal populations return to their historical breeding grounds, it is expected that there will be increased levels of interaction between humans and seals in

areas that are visited by humans for recreational purposes including tourism (Boren *et al.* 2002). Increasing numbers of seals on coastal highways resulted in road deaths from collisions with cars (Boren, Morrissey & Gemmell 2008), and increases in seal numbers near towns may increase the frequency of vehicle accidents in urban areas. The recent recolonization of the coastal areas of the Otago peninsula by the New Zealand fur seals and the New Zealand sea lion has resulted in an increase in interactions between the public and the seals. For example, the animals have been sighted in urban areas, waterways and beaches, increasing the rate of human-seal encounters; this has resulted in the public perception of the animals as a threat to public health and vermin (Lalas 2008). The ability to identify potential problem areas in advance through predicting the direction and timing of fur seal population expansions, and designing management strategies in accordance to this would be a valuable skill in minimizing the human-wildlife conflict (Bradshaw *et al.* 1999; Bradshaw *et al.* 2002).

Statement of the problem

Past studies on the conspecific aggression in various species of pinnipeds have concentrated on its functions, but no research has focused on the effects of conspecific aggression on the spatial population dynamics. The aim of this thesis is to investigate the latter to better determine the effects of population increases on current breeding colonies of New Zealand fur seals. Although numerous studies have focused on the functions of female aggression in well-studied species such as the northern fur seal *Callorhinus ursinus; (Francis 1987)* and the South American fur seal; (Harcourt 1992b; Cassini & Fernández-Juricic 2003; Fernández-Juricic & Cassini 2007), no research has been performed as of yet to attempt to quantify the aggression behaviour in the form of aggression distance in otariids, and work on New Zealand fur seals is relatively scarce (Lalas & Bradshaw 2001). Due to the differences in the breeding ecology and social behaviour between the otariids and phocids, the functions of aggression in the New Zealand fur seal are likely to differ from the functions of aggression learned from previous work. Additionally, some studies have focused on the identification and assessment of preferred breeding locations and substrates (e.g., Ryan *et al.* 1997); however, no methodology has been developed to track or estimate the number of breeding New Zealand fur seal individuals that a given habitat area can sustain. This

highlights the current inability to make predictions in regards to the time of the expansion of a rookery.

Thesis aims

The primary objective of this research is to quantify the breeding territory size of female New Zealand fur seals by examining the intra-species aggression distance. This study will also contribute to the current scientific knowledge of pinniped behaviour, by investigating the functions of intra-species and intra-sexual aggression in female New Zealand fur seals.

To investigate the carrying capacity of a New Zealand fur seal rookery in relation to the breeding population, I will explore the female aggression behaviour, and the resulting female territory size as the limiting factor. Adult female fur seals are the numerically dominant sex and age group in rookeries during the peak period of the number of territorial individuals (pupping period) (Stirling 1971; Miller 1975; Shaughnessy *et al.* 1994; Harcourt 2001; Boren 2005), and thus the demographic group which occupy the most space in the rookery. Therefore, it can be safely assumed that the number of females in a rookery during the pupping period will be the primary factor that drives the growth and expansion of the rookery.

The study objectives are:

1. To investigate the functions of aggression in female New Zealand fur seals, and compare with previous studies on conspecific aggression in other pinniped species.
2. To assess the use of conspecific aggression measurements in estimating colony density and dispersion of individuals.
3. To explore the implications of conspecific aggression on the spatial population dynamics of colonial species.

This study of the aggression behaviour in the female fur seals is expected to assist in the production of the New Zealand fur seal population management and fisheries management plans, by providing information in regards to population dynamics and

rookery carrying capacity. This information is expected to be useful for management planning as it will help predict the time and direction of rookery expansion, allowing an evaluation of the areas that may require management attention in the future.

Previous researches have shown that the functions of female aggression can significantly differ between different species of pinnipeds (e.g., Christenson & Le Boeuf 1978; Boness *et al.* 1982; Carey 1992). Therefore, this study will also provide a good opportunity for behavioural comparisons between different fur seal species, and why some of these behavioural differences may occur. There also has been limited research on the aggression in New Zealand fur seals; a previous work has focussed on thermoregulation and space defence (Carey 1992), but no other potential functions of aggression have been explored. Further research would contribute to the current scientific knowledge, and either provide support to the existing hypotheses or present novel hypotheses for the functions of aggression in female fur seals.

Methods

Ohau Point seal colony

Female New Zealand fur seals (*Arctocephalus forsteri*) were observed at the Ohau Point seal colony which is located 26kms north of Kaikoura, on the East coast of New Zealand's South Island (Figure 1). The period of observation was from November 2014 to April 2015. The seal colony is a rookery; a site used for breeding purposes. Ohau Point seal colony is the largest fur seal breeding colony in Kaikoura, with an estimated 3000 individuals and an annual pup production of approx. 600 as of 2005 (Boren *et al.* 2006; Boren *et al.* 2008). The rookery is situated adjacent to a highway and spans about 1 km of the coastline. Parts of the rookery are located under coastal cliffs; some formed of natural rocks and some formed of man-made walls for the highway.

The study area, named North Platform or sub-site no. 3 in previous studies (L. Boren, personal communication; Boren *et al.* 2002), was chosen as the primary research location (Figure 2). This was based on the presence of a good vantage point, good visual access to most areas of the site due to the lack of caves or large crevices, distinct physical partial barriers to neighbouring sites, various substrate types, presence of tidal and non-tidal pools, and the high number of female seals in the area. The study area was c. 54.2 m long and 27 m wide (from the cliff to the furthest dry ledge at high tide) which equates to 1463.4 m^2.(ImageJ drawn size 1330 m^2). At low tide, the width of the study area expanded to 34 m to include the exposed tidal rocks. The vantage point used for observations was on top of a man-made concrete wall c. 7.8 m high. Depending on the location of the individuals chosen, the distance from the observer to the subject individuals ranged from 7.8 m to 35 m from the vantage point to the tidal rocks. The site consisted of various types of rocky substrates, such as smooth rock surfaces, stony clearings, steep clusters of large rocks, and formations of large boulders. The study area was relatively protected from wave by offshore reefs. The site had one large pool during the high tide and four extra tidal pools during the low tide.

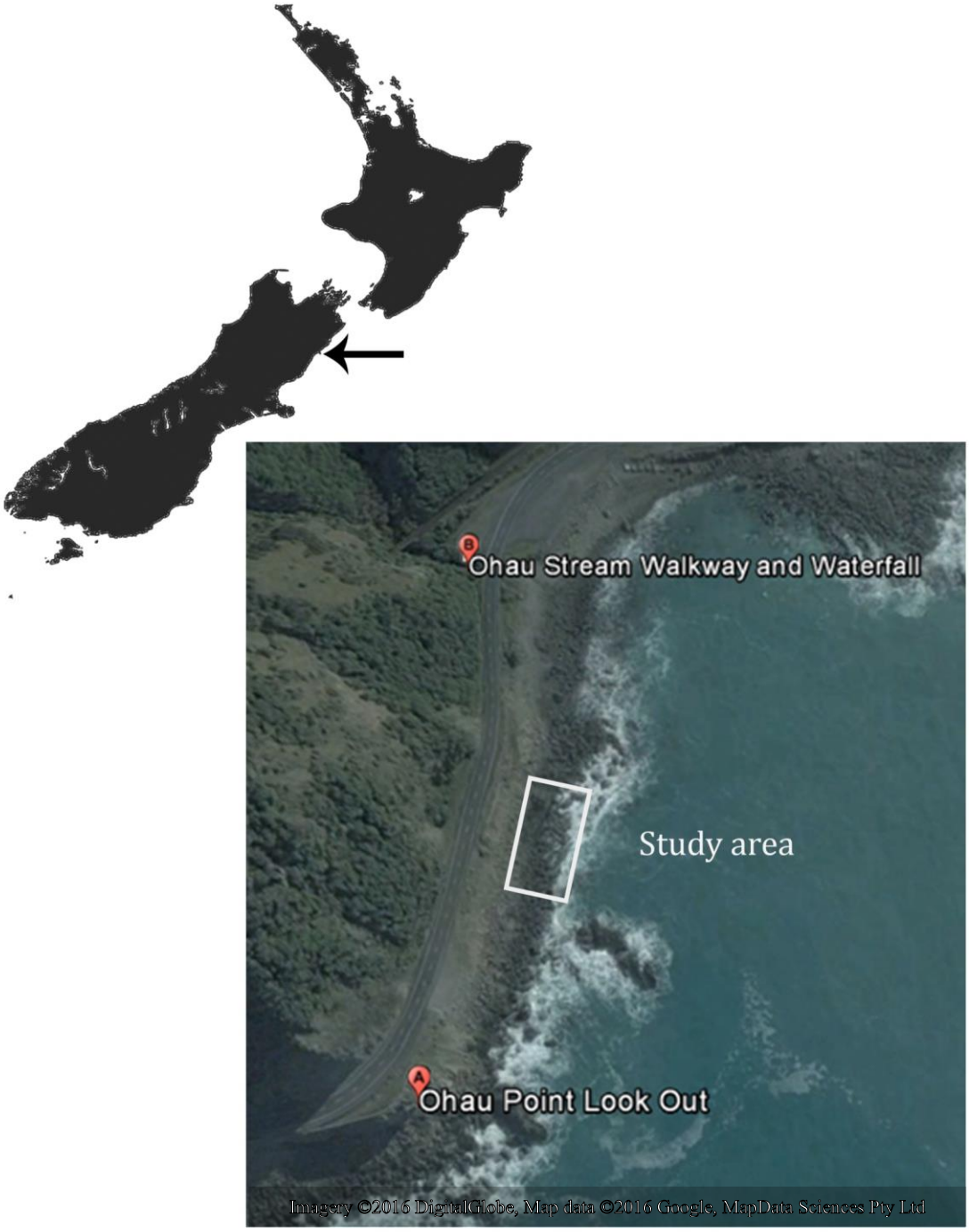

Figure 1. Map of New Zealand with an arrow marking the location of Kaikoura. Google Earth imagery shows a bird's eye view of the Ohau Point seal colony, with the study area marked with a white rectangle.

Figure 2. Study area at mid-high tide, looking down from the vantage point. This view shows most of the study area, with the north and south borders of the area within c. 5 m from the left and right edges of the image. The primary pool can be seen near the center of the image.

Sampling methods

Behavioural data were captured both on video and with still photography. Sampling occurred on three days of each week for a period of 5 months, and the sampling days were chosen using a random number generator. Three one hour sampling sessions occurred per sampling day at 7 am, 12 pm and 6 pm, to allow for observation of differences in seal behaviour during different times of the day. After the change in daylight savings time, the afternoon sessions were moved to begin at 5 pm due to the lack of natural light, which significantly reduced visibility. I was unable to sample for the evening sampling time on the 11th of February due to road closure.

A Panasonic HC-V550M video camera mounted on a tripod was used to film during all sampling sessions. Additionally the entire study area, showing the locations of all seals visible from the vantage point, was photographically documented at the beginning of the sampling sessions using a Fujifilm Finepix s2950 and a Canon EOS 1100 digital camera.

Focal-animal sampling

I used the focal-animal sampling (Altmann 1974) where a focal female and pup pair were filmed for the entire sampling session. To minimize pseudo-replication, pairs at various locations within the study area were chosen for each sampling time, as many species of pinnipeds are known to exhibit small-scale site fidelity to some degree (Lunn & Boyd 1991; Pomeroy *et al.* 1994; Wolf & Trillmich 2007; Parker *et al.* 2008). Individuals at locations that had been filmed on the same or the previous day were avoided, unless the pair was identified as different individuals by their tags or markings. A female and a pup were determined as mother and pup by observing their interactions (suckling, playing, and other interactive behaviour without aggression from the female resulting in pup being driven away) or if they were resting within 0.5 m of each other (McNab & Crawley 1975; Francis 1987). By choosing only the females with her pup, I ensured that all focal females in my study were lactating females. If the focal pair moved or separated, I continued to film and observe the behaviour of the focal female, not the focal pup. If the focal female was lost from view or if she left the colony within the first 45 min of the sampling period, a new focal pair was chosen and sampling began again from the start.

The total number of adult males, adult females, yearlings, new-born pups and juveniles visible within the study area were counted and recorded at the start of each sampling session. Identification of seals of different ages and sexes were done using descriptors from past studies, as indicated below (Crawley & Wilson 1976; Wilson 1981; L. Boren, personal communication, 2015; Goldsworthy & Shaughnessy 1994; Dickie & Dawson 2003).

New-born pups (pups born in the current breeding season): body length of c. 40 cm at birth, usually with dark black coat until moulting at age of about 5 to 6 months old.

Yearlings: body length of less than 1 m, usually with light grey coat with yellow tinges.

Juveniles: body length of less than 1 m, usually with silvery-grey or brown adult coats.

Females (adults): body length of 1 to 1.5 m with slender body shape and neck.

Sub-dominant males: body length greater than 1 m, with head and neck larger than those of females, but without the distinctively massive necks of dominant males. The size of males under the age of 5 are thought to not greatly differ from adult females (Dickie & Dawson 2003). The presence of the mane around the neck and the size and shape of the fore-flippers were also used as more reliable identifiers.

Dominant males (adults): body length of 1.5 to 2 m, with a distinctively large neck, especially during breeding season, which is covered with fur thicker and longer than the rest of the body. Are able to establish and defend territories from other males.

The following abiotic factors were visually estimated and noted at the beginning of each session: tide state (low, mid, high); percent cloud cover; wind speed; and sea roughness. In addition, I calculated and noted tide levels (meters) for the corresponding sampling time using the Kaikoura Tide Chart provided by Metservice (www.metservice.co.nz). The tide states recorded at each sampling session were used for comparison and as reference when calculating the tide levels from the tide chart. Both the wind speed and sea roughness were noted in five levels, from mild/low to strong/rough. The rock temperature at the colony was measured during each sampling time using an Onset HOBO Data Logger pendant setup tied to a small fishing rod, which was cast from the vantage point into the study area. The logger pendant setup consisted of the pendant protected in a loose cone-shaped casing of plastic gutter guard with a small parachute attached at the top end to slow the fall. This setup was devised for the protection of the logger pendants after experiencing impact damage early in the study period. The data logger was set up to record temperature every 10 s, and the temperature logs taken for the duration of each sampling were calculated to yield the mean temperature for each sampling times. Due to malfunctions of the data logger or external damage, temperature logs from 12 out of 184 sampling times (6.5%) were lost.

A 1 m wooden plank was used as a 1 m scale for measurements, by being placed at various sites within the study area and filmed at different zoom levels. The plank was filmed in both horizontal and vertical positions, placed as level as possible with the rocky surface. The plank was sprayed with black matte finish spray paint to increase light absorption. This was done as the natural wood, gloss or other bright colour could have produced inaccurate measurements due to reflection of sunlight. Study area

measurements were also taken and were used as a reference to calculate the total length and width of the study area using ImageJ.

Identification of individuals

A number of adult seals could be visually identified. Some females with round yellow tags could be distinguished from non-tagged females and from each other by the presence and location of the tag (left or right flipper). Some females were observed with rectangular tags, with the numbers visible in photographic data. Allflex ® sheep-tags with four-digit numbers were identified as females tagged in a previous study in the same location 10 – 14 y prior (Boren 2005). Other females were identified by unique markings, such as white spots on their heads and foreheads, spots on their backs (presumed to be a change in fur colour due to an injury) or scars (Figure 3). For about three weeks from the 1st of January 2015, some pups could be identified from numbered tags that were applied for research occurring concurrently (O. Gooday), and this allowed reliable identification of females if a tagged pup was seen with its mother. From March 2015, some pups were again able to be identified by haircut markings also applied for Gooday's research. The presence of all visually identifiable individuals was noted during observation and documented photographically if possible, allowing further confirmation and study of the distinguishable individuals. At times, I was unable to photographically document some individuals due to the seals lying or sitting in a way that concealed the tags or markings that were visually noted, the lack of available photography equipment, and/or due to the animal leaving the study area before photography equipment became available.

Figure 3. Examples of identifiable female New Zealand fur seals. **a.** Female with a yellow Allflex ® tag on the posterior edge of her right flipper. **b.** Female with light coloured spots on the forehead and near the rump.

Quantification of agonistic interactions

All videos were scored for the frequency of female aggression, aggression intensity and the distances at the onset of each agonistic and non-agonistic response to an approaching conspecific using the video playback program GOM Media Player. During the behaviour scoring, the sex and age group of the approaching individual was noted and the time points at which the focal female responded were noted as encounter 1, encounter 2, and so on. The sex and age group of the approaching individuals were noted as dominant male, young male, adult female, juvenile, yearling, and new-born pup. The four intensities of aggression from the focal female were noted within each encounter for the exhibition of the following behaviours:

Threat: An open-mouth threat, where the individual opens its mouth and shows its teeth while facing the general direction of the opponent. This behaviour may or may not be accompanied by a growl (Figure 4a).

Threat-exaggeration: A behaviour that appears to emphasize the threat by extending the neck towards the general direction of the opponent while displaying threat behaviour, similar to the 'horizontal neck-stretch' behaviour of the Southern Australian population of *A.forsteri* (Stirling 1971). This behaviour appears to have been categorized with either 'threat' or 'lunge' in a number of past studies on pinniped aggression (Boness *et al.* 1982; Francis 1987; Carey 1992). However, I decided to categorize this behaviour as separate, as I noted some distinguishable behavioural components that differed from 'lunge' as previously defined by the studies cited above (Carey 1992), as 'lunge' was usually displayed when opponent was within reach, while 'threat-exaggeration' usually occurred when opponent was out of reach (Figure 4b).

Lunge: A quick extension of the neck (while displaying threat behaviour) towards a specific body part of the opponent, with a snapping motion of the jaw but without contact. This behaviour was usually observed when the opponent was in close proximity of the focal individual, normally within the reach of the focal individual's snout. When this behaviour was displayed towards an opponent that was not within the reach of the focal female, it was accompanied by the focal female moving closer to

the opponent. This behaviour is thought to facilitate body contact to allow biting (Figure 4c).

Bite: Contact between the focal individual's open mouth and the opponent's body, with the focal individual's mouth closing while still in contact. This behaviour almost always causes the opponent to yelp, scramble to move away, or a quick movement of the targeted body part away from the aggressor and/or a lunge towards the head of the aggressor. However, from personal observation, bites from adult females hardly ever produced any of these responses from dominant males, instead being simply ignored (Figure 4d).

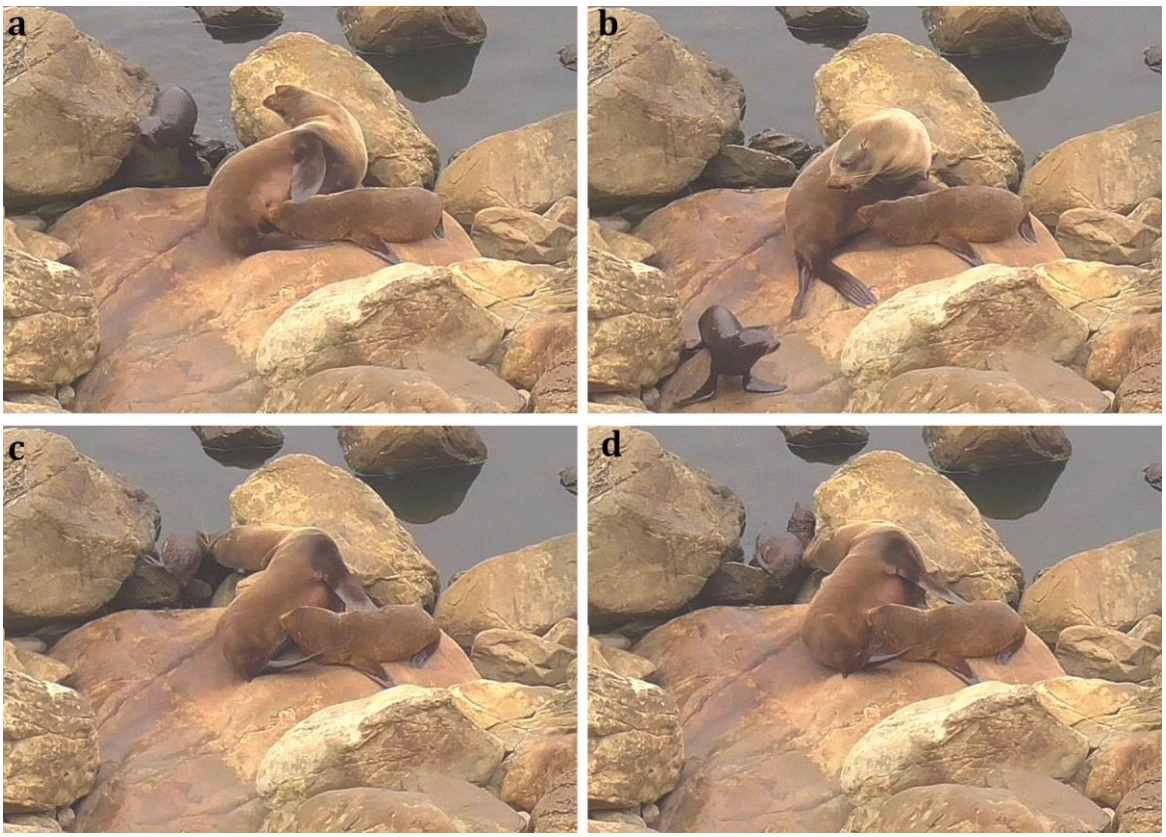

Figure 4. a. Threat behaviour shown by the focal female (center of image) with her pup (dry pup suckling from the female) towards a non-filial pup (wet pup left of the female, emerging out from the pool). **b.** Threat-exaggeration from the focal female to the non-filial pup, with her neck elongated towards the opponent. **c.** Lunge behaviour in progress, as the female orients her mouth towards the opponent and elongates neck in an attempt to make contact. The opponent is in the process of returning to the pool. **d.** Bite, as lunge results in a contact with the opponent and mouth grabs a part of the opponent.

Other behaviours such as *'neck-waving'* (females pushing their chests against each other, while waving their necks: Carey 1992) and '*chase'* (female chasing after a withdrawing individual, usually post-aggression: Carey 1992) were also noted; however, these were not included in the analyses due to their low rate of occurrence. Instances where the focal female did not show any form of response (i.e. opening of eyes, head movement or gaze following the movement of opponent) to approaching or passing conspecifics were noted as 'no response'. If multiple encounters occurred with the same individual approaching the focal female, this was noted for subsequent encounters only when it could be confirmed as the same individual.

To acquire accurate measurements for the various site areas at which the focal females were filmed, the 1 m scale at the appropriate zoom level from the closest area was chosen and used as a 1 m reference. As the video recordings of the 1 m scale did not cover every zoom level that was used in videoing the focal females, the 1 m distance in some zoom levels was estimated by calculating the difference in the lengths of certain markers such as rocks of known size from other zoom levels.

Screen Caliper, an on-screen measurement tool, was used to create a grid with PhiMatrix, an on-screen grid program. This was done by placing a Screen Caliper at a horizontal angle showing the horizontal 1 m length and another Screen Caliper showing the vertical 1 m length for the zoom level of the video being processed. The top left corner of a PhiMatrix grid was placed on the Screen Caliper and resized so that 4 squares would fit in each of the Screen Caliper, resulting in a 0.25 x 0.25 m grid for the site area and zoom level of the video being processed. The grids tended to be rectangles elongated horizontally, as the vertical laying of the plank at level with the ground made it appear shortened at most site areas. This grid was overlaid on the video during playback for quick distance estimation (Figure 5). Distances were scored to the nearest 0.125 m starting from 0 m (contact) to 0.25 m, then to the nearest 0.25 m starting from 0.25 m to 3 m. Screen Caliper was used in conjunction with PhiMatrix to estimate distances between the seals.

Response distance, the non-agonistic response, was measured at the initial point of response of the focal female to an approaching seal, while the aggression distance was measured at each onset of aggression behaviours; threat, threat exaggeration, lunge and

bite. Other variables noted during the video processing were: the orientation of the approaching seal (noted as moving towards focal, passing by focal and moving away from focal), the direction at which a seal approached a focal female (noted as from head, back, belly, flank and tail) and the presence or absence of focal pup.

During the scoring process I also noted the presence of the focal female's filial pup, whether the filial pup was suckling, the number of individuals within a 2 m radius of the focal female including their sex and age group (number of neighbours) and the distance of each of these neighbours from the focal female. The distance of the neighbours from the focal female was calculated in increments of 0.25 m. Additionally, the time points were noted for non-focal female aggression, pup-to-pup aggression, and when the focal female did not respond to individuals approaching within 1 m (no-response). Multiple snapshots from the videos were saved as image files with the dates, session time and zoom levels to allow future reference to the location of the focal female, body size measurements, and easy identification of distinguishable females.

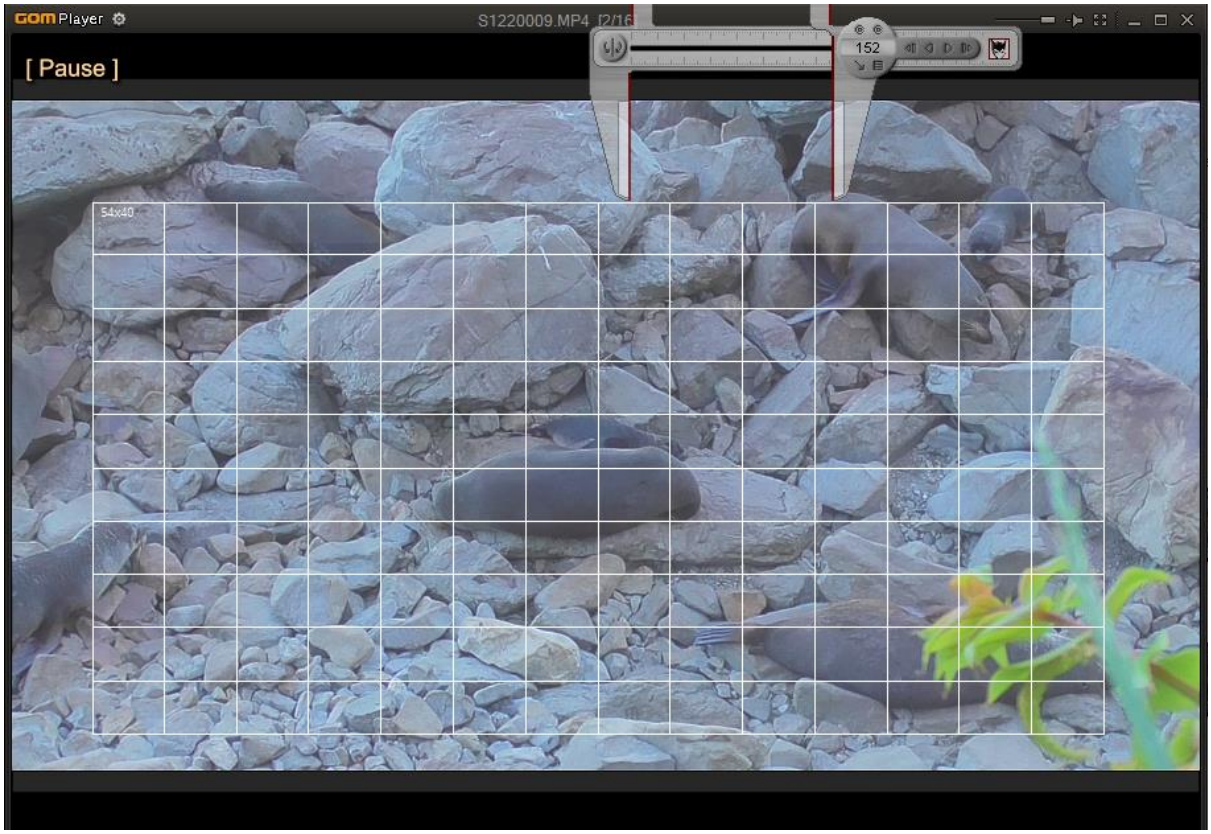

Figure 5. Example of aggression distance measurement process using PhiMatrix grid (white grid in the center) and Screen Caliper (caliper shown in the upper area), with GOM Media Player used for video playback. Focal female at the center of the image with filial pup.

Pup presence

By referring to the notes taken of the presence and absence of the focal females' offspring for every aggressive encounter during the second video processing, I extracted a set of focal female samples which responded to conspecifics in both the presence and absence of their pups. This was done to ensure comparisons in the behaviour of each focal female in the presence and absence of filial offspring, eliminating the potential for the results to be biased from inter-individual variations. The mean response and aggression distance for all interactions which occurred either in the presence or absence of the focal offspring were used for subsequent analysis. As not all focal female responses lead to an aggressive behaviour, the set of data showing the mean aggression distance in the presence and absence of focal offspring was inevitably smaller than the mean response distance data. Then, to analyse inter-female aggression in the presence and absence of focal offspring, I calculated the mean of the response and aggression data only from the interactions in which the non-focal animal was an adult female.

Focal female location

Using the video recordings and screenshots of video recordings, the locations of focal females at the time of recording were identified and noted. To obtain more accurate results, only the sampling times where the female stayed in one location for the entire duration of the recording were used for statistical analyses. The rock sizes on which the focal females were resting were also recorded from the videos as < 0.25 m, c. 0.5 m, c. 1 m, c. 2 m, and > 5 m, with the rock size of > 5 m being areas of smooth rock formation around the seaward edge of the study area. The image of the entire study area was produced from screenshots from a quadcopter video of the colony (kindly provided by O. Gooday) which were joined together using the photo stitching software PTGui. The numerical identifiers of each focal female were overlaid on the study area image at their respective locations using Adobe Photoshop. I then measured the distance (m) to the closest pool and to the sea from each of the focal female's location using ImageJ, using a set distance which was measured between two identifiable markers as a scale.

Birthing and nursing periods

The first confirmed presence of a new-born pup within my study area was on the 24th November 2014, The last birth or indications of recent birthing was observed in the study area on the 28th of December 2014, which was used as the last day of the birthing period of my study population. Therefore, the identified birthing period of the study population was from the 24th November to 28th December, and the nursing period was from the 29th December to the end of the study period, 23rd of April 2015. These dates were used to compare the behaviour and location of the seals between these periods throughout the analysis of data.

Mapping of site occupancy

To accurately determine the zones within the study area that were used for pupping, the photos of the study area from thirteen sampling times during the birthing period were used to map the area usage by reproductive females (Figure 6). Only the females seen in resting or nursing positions with pups were used in the mapping and any female-pup pairs in a moving position or solitary pups were excluded; this was to ensure that all mapped sites were of female choice. Using Adobe Photoshop, the outline of all the sites used for birthing and nursing was deduced from this set of maps, and its zone was measured using ImageJ, with a measurement between two distinct points taken in the study area as a reference for scale. The mean aggression distance was used to calculate the mean individual territory size (defined here as the defended area around an individual), while the mean nearest-female neighbour distance was used to obtain the size of the individual space (defined here as the space in which no other seals were established, this space was often smaller than the defended territory size) respectively. The mean territory size was calculated from the mean of all focal females' averaged length of aggression distance, while the mean nearest- female neighbour distance was a mean of the distance between all focal females and their nearest female neighbours. The nearest-female neighbour distance data was obtained from the distance measurements of all neighbours of the focal females thus was in increments of 0.25 m. By using these measurements coupled with the average female New Zealand fur seal body measurements of 1.17 m length (Dickie & Dawson 2003) and 0.5 m body width, the area

size which each female would occupy and defend (territory size), and the occupied area size of each focal female (individual space) were obtained. The female body width was measured from the video data from this study, using the same methods as the measurements of response and aggression distances. The body width (chest) was measured in 12 females, and the body width including the flippers was measured in 5 of these females (females which untucked their flippers from under the body and had them extended flat on the ground during the filming). Only the females near the vantage point and at the exact locations where the 1 m scale was positioned were used in the body width measurement to maximise accuracy. The mean territory size and the mean individual space size were then calculated for birthing period and the nursing period, to predict the number of females that the study area would be expected to be able to support, and compare the results to the actual counts.

Figure 6. Bird's eye view of the study area at mid-tide, created from a video taken by a quadcopter (kindly provided by O.Gooday) using PTGui and Adobe Photoshop. White outline shows the birthing area, mapped by referring to site occupancy of all established females with pups born during the 2014 – 2015 season which were observed between 24 Nov to 21 Dec. Yellow circles each represent a sighting of a nursing female outside the primary birthing area. The blue lines show the northern (left) and southern (right) borders of the study area, while the bottom line shows the bottom edge of the cliff.

Data Analysis

Preparation of data

Response frequency is the total number of times the focal female responded to an approaching seal (opponent). The data from the sampling periods that yielded response distance, but no aggression distance (instances in which the focal female showed response to an approaching individual, but no aggression was shown) were included in the response distance analyses, and excluded in the aggression distance analyses. Most of the focal females were involved in numerous interactions each, resulting in multiple measures of response and aggression distances per female. Therefore, the means of the response and aggression distance were calculated for each female, resulting in 176 samples for the response distance and 165 samples for the aggression distance.

Rather than the rate of aggression which was widely used in previous studies of female aggression in pinnipeds (e.g., Cox 1981; Carey 1992; Neumann 1999; Cassini 2001; Fernández-Juricic & Cassini 2007; Young *et al.* 2008), the proportion of aggression was used as a measure of the females' degree of aggressiveness along with the aggression distance. This is because unlike the rate of aggression, the proportion of aggression is not influenced by the total number of potential interactions (number of responses). For example, an increase in the number of responses will increase the chances of aggressive interactions to occur, which can result in a higher number of aggressive interactions. Conversely, if the number of responses was low, it imposes a limit on the number of aggressive interactions. However, the proportion of aggression represents the likelihood that the focal animal will display a certain amount of aggression per set of responses, thus yielding the true degree of aggressiveness. The proportion of aggression was the number of aggressive interactions from the total number of interactions.

$$\frac{\text{Number of aggressive interactions}}{\text{Number of responses}} = \text{Proportion of aggression}$$

Statistical analysis

The statistical program R version 3.0.3 (R Development Core Team 2015) was used for all analyses. The primary objective of the statistical analysis was to test the response and aggression distances given a range of biotic and environmental factors. All data from all encounters during the entire season was used for statistical analyses. Shapiro tests (Shapiro & Wilk 1965) were used to test for normality, but these data sets were not normally distributed. As response distance data could not be normalized using transformations, it was normalised with the interquartile (IQR) outlier deletion method (Sunitha *et al.* 2014). The IQR outlier deletion method allowed me to retain as much of the intact data as possible. Aggression distance data was normalised using log transformation.

The proportion of aggression, and the frequency of responses data were not able to be normalized using log transform or square-root transform; therefore, nonparametric regression using R package 'np' was used (Hayfield & Racine 2008).

For the environmental factors, time of day, rock temperature, wind speed, tide level (meters), wave height and cloud cover (%) were included in the analysis. The wind speed and wave height which were visually noted were given scores of 1 to 5 (1 being calm and 5 being strong/rough) for the analyses. Multiple linear regression, nonparametric regression, ordered logistic regression using R package 'MASS' (Venables & Ripley 2002), Analysis of Variance (ANOVA), and Kruskal-Wallis tests were used to analyse the effect of these predictors on response distance, aggression distance, frequency of responses and the proportion of aggression and the highest level of aggression shown.

The biotic predictors used in these analyses were: encounter number (total response bouts from the focal female towards approaching seals); proportion of aggression (proportion of aggressive encounters out of all encounters by the focal female); study area population size (the number of seals that were counted as present in the study area at the beginning of every sampling period); number of nearby seals (the number of seals within a 2 m radius of the focal female at the beginning of the sampling time, counted from the video recordings); and the number of no responses (the number of times where the focal female did not show any response to approaching or passing seals

within 1 m of her). Multiple linear regressions, nonparametric regressions, ANOVA and Kruskal-Wallis tests were used for the analysis of these predictors against the mean response distance, mean aggression distance, the frequency of responses and proportion of aggression.

The relationships between the mean response and aggression distances of females and the number of dominant males in the study area were analysed using simple linear regression, while the relationships of the response distance, aggression distance and proportion of aggression to the presence of dominant males in the vicinity (< 2 m) of the focal females were analysed using ANOVA and Mann-Whitney-Wilcoxon test.

The mean response distance between the presence and absence of offspring was analysed for each of the response distances towards all approaching seals, adult females, and non-filial pups. A two sample t-test was used if not normally distributed data could be normalized with square root transformation, and Mann-Whitney-Wilcoxon tests were used if the data could not be normalized. The same methods and tests were used to investigate the relationship of the mean aggression distance to all approaching seals, adult females or non-filial pups between the presence and absence of offspring.

Simple linear regression was used for assessing the relationship between the distance of the focal female from the sea and the closest tide pool on the mean response and aggression distances. Simple linear regression was also used to investigate the relationship of temperature and the distance of the focal female from the sea and the closest pool. ANOVA was used to investigate the effects of different rock sizes in the focal areas on the response and aggression distance of the focal females in the respective areas. Two sample t-tests and Mann-Whitney-Wilcoxon tests were used to compare the distance of the focal female from the sea and the closest pool, and the rock sizes, between the birthing and the nursing periods. The two sample t-tests and Mann-Whitney-Wilcoxon tests were also used to compare the mean response distance, aggression distance, the proportion of aggression, study area female population and the number of female neighbours between the birthing and the nursing periods. Simple linear regression, nonparametric regression and ordinal logistic regression tests were used to investigate the effects of the number of males on the focal females' distance from the sea, nearest pool and the rock size. Nonparametric regression and Kruskal-

Wallis tests were used to test the effects of the distance to the sea, nearest pool and the rock size on the total number of neighbours and the number of female neighbours.

Finally, the nearest female neighbour distance data was not able to be normalised; therefore, the effects of the environmental predictors, biotic predictors, focal female location data and the response and aggression distances were tested using ordinal logistic regression and Kruskal-Wallis tests, while Mann-Whitney-Wilcoxon test was used for its comparison between the birthing and the nursing periods.

Results

The rate of encounter of focal females with seals of both sexes and ages was 15 ± 1 per h (± SE) (range 0 – 88) and with adult females (when a minimum of one female was encountered) it was 4.78 ± 0.48 per h (1 – 31). The rate of aggressive encounters with seals of both sexes and ages was 8.24 ± 0.6 per h (0 – 50) and with adult females this was 2.76 ± 0.34 per h (0 – 21). The response distance of focal females towards all approaching seals over the entire study period was 0.64 ± 0.0 2 m (0 – 2.5 m), while the average aggression distance was 0.46 ± 0.02 m (0.125 – 2 m).

Environmental influences on behaviour

Response frequency increased with increases in rock temperature (n= 172, Bandwidth= 121415785, p= 0.003; Figure 7a, Table 1) and was significantly higher during midday (n= 184, H(2)= 10.056, P= 0.006; Figure 7b, Table 1). The response frequency did not show a significant relationship with any other environmental predictors (Table 1).

Tide level, wind speed, wave height or percentage of cloud cover did not have a significant effect on the response distance (Table 2) nor on the aggression distance of focal females (Table 3). However, rock temperature had significantly negative effects on both response (n= 165, t= -2.106, p= 0.037; Figure 8a, Table 2) and aggression (n= 165, t= -2.003, p= 0.047; Figure 8b, Table 3) distance.

The proportion of aggressive behaviour significantly increased with an increase in rock temperature (n= 165, t= 2.18, p= 0.03; Figure 9a,

Table 4), significantly affected by percentage of cloud cover (Figure 9b,

Table 4) and was significantly higher during midday (n= 176, H(2)= 12.366, p= 0.002; Figure 9c,

Table 4).

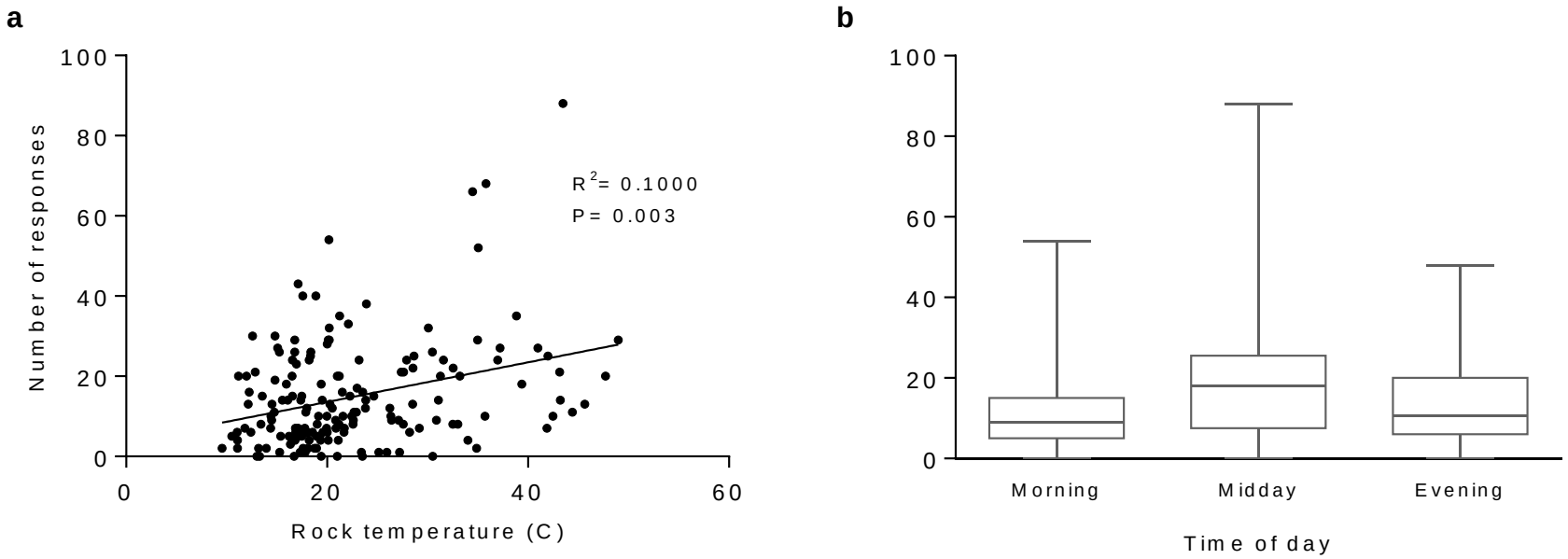

Figure 7. Number of focal female responses (m) as a factor of **a.** rock temperature and **b.** time of day.

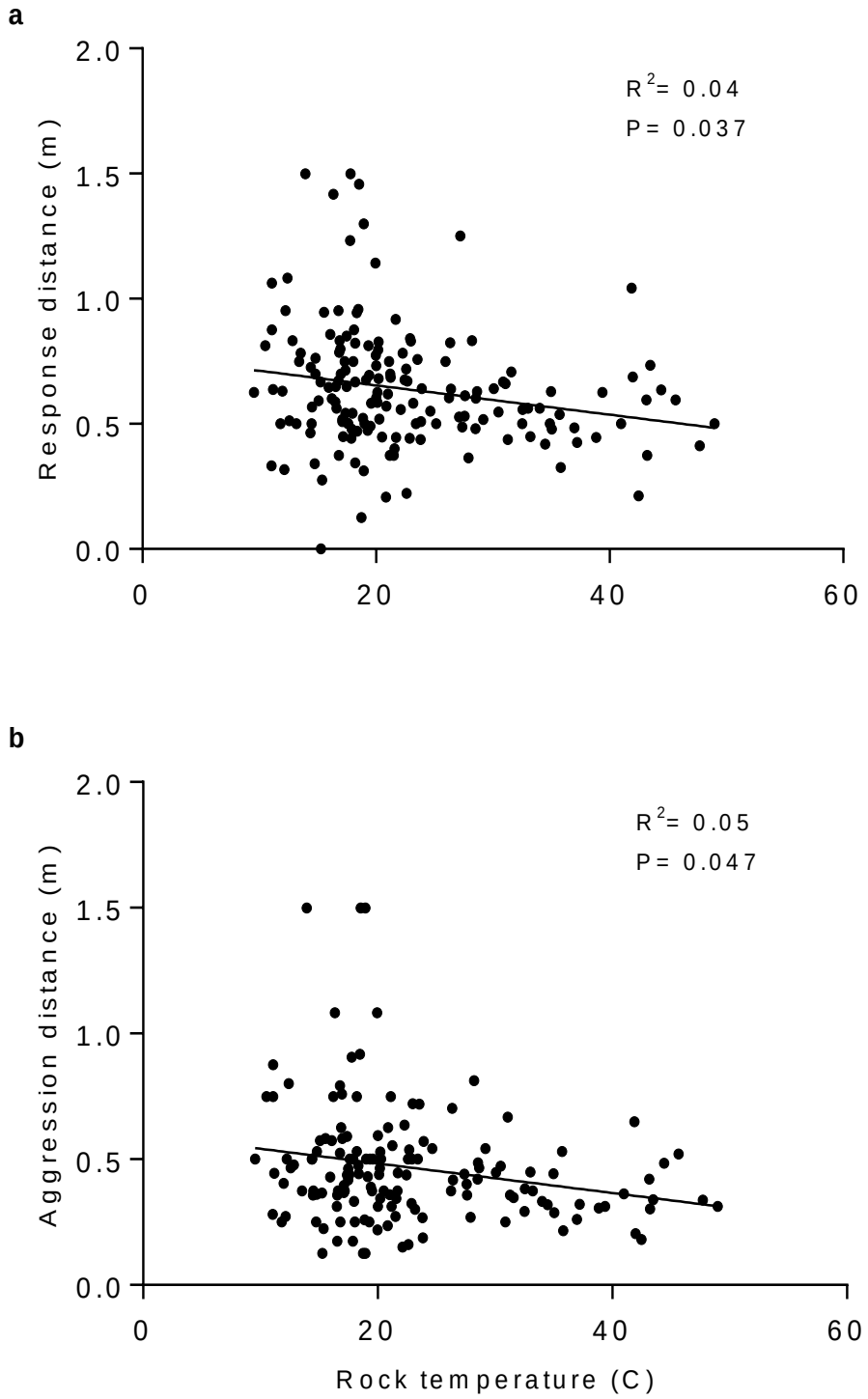

Figure 8. a. Focal females' response distance (m) as a factor of rock temperature. **b.** Focal females' aggression distance (m) as a factor of rock temperature.

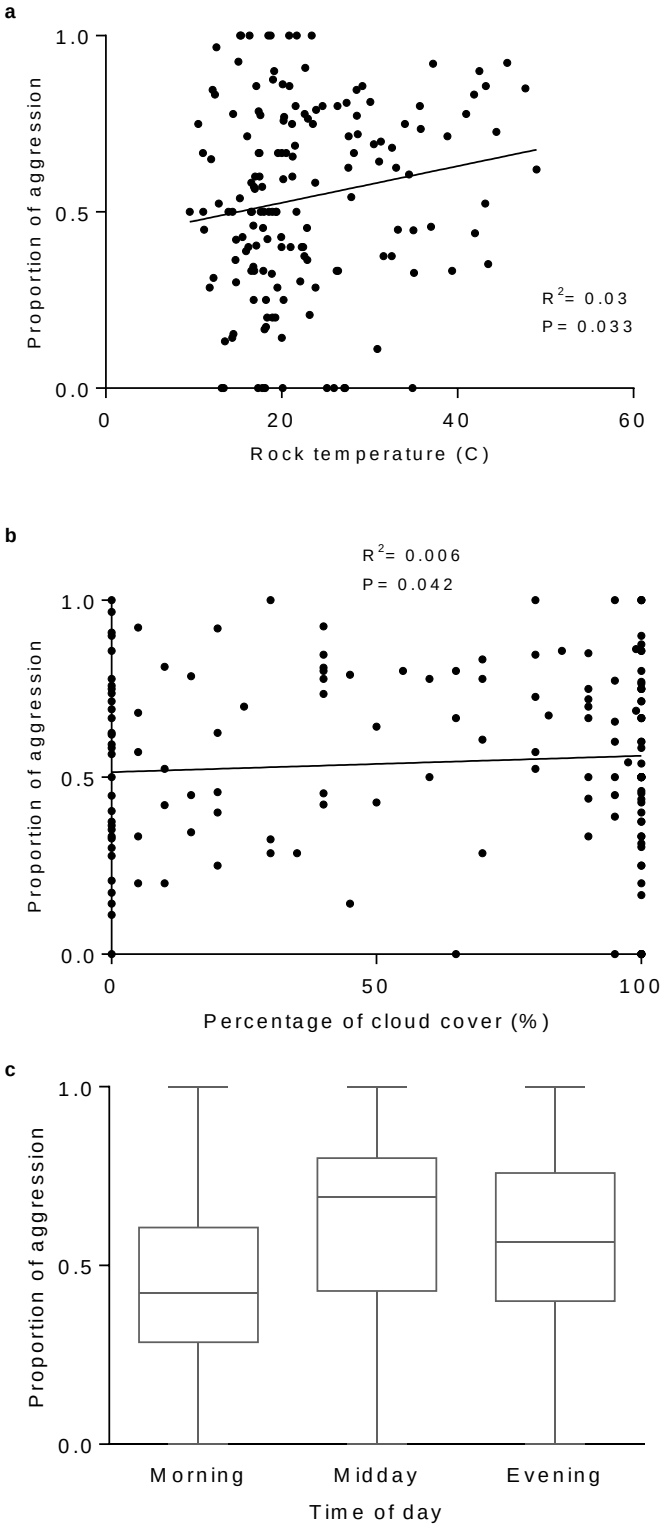

Figure 9. **a.** Proportion of focal female aggression as a factor of rock temperature**. b**. Proportion of focal female aggression as a factor of cloud cover. **c**. Proportion of focal female aggression as a factor of time of day.

Furthermore, the focal females' highest intensity of aggression displayed a weak relationship with rock temperature (n= 154, t= 1.98, p= 0.048; Figure 10), with the relationship between threat exaggeration and lunge being non- significant (t= 1.58, p= 0.114) and the relationship between lunge and bite being highly significant (t= 4.75, p <0.0001).

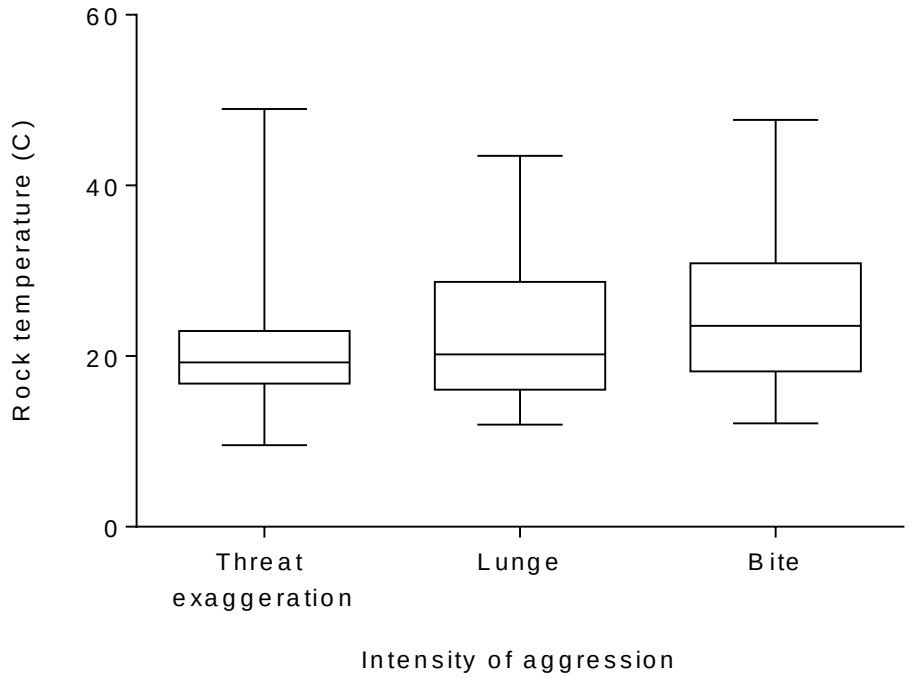

Figure 10. Highest intensity of aggression displayed by focal females as a factor of rock temperature.

Neither the response distance (n=176, W= 2266.5, p= 0.296) or the aggression distance (n= 165, W= 1730. P= 0.862) differed between the birthing period (24 November to 28 December 2014) and the nursing period (29 December 2014 to 23 April 2015). There was also no significant difference in the proportion of aggression between the birthing and the nursing period (n= 176, W= 2285.5, p= 0.256). The rock temperature also did not significantly vary between the birthing and the nursing periods (n= 175, W= 1465.5, p= 0.8). There was considerable variation in rock temperature over the study period and between the times of day (Figure 11).

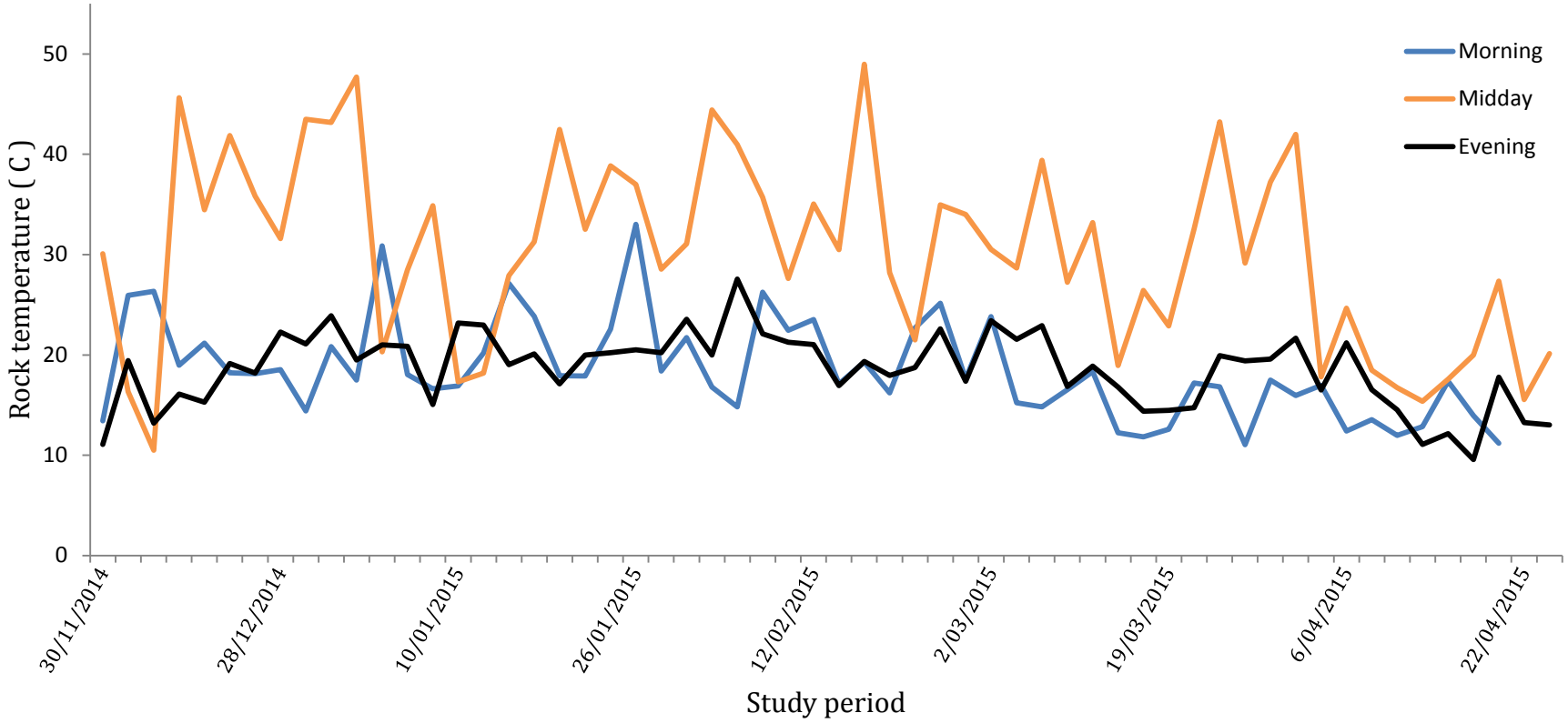

Figure 11. Rock temperature recorded at the study site during the study period shown as different times of day. The highest rock temperatures were recorded during mid-day, but rock temperature greatly varied over the study period.

Biotic influences on behaviour

The mean population size of the study area was 134.8 individuals (range 48 – 198). The mean number of males was 3.5 individuals (0 – 14). The mean number of females was 43.5 individuals (11 – 105). The highest number of pups counted during the birthing period was 102, while the highest number of pups counted during the nursing period was 149.

The mean population size of the study area during the birthing period was 143.6 (range 48 – 196) and 133.2 (69 – 198) during the nursing period. The mean number of males during the birthing period was 10.6 (6 – 14) and 2.1 (0 – 9) during the nursing period. The mean number of females during the birthing period was 74 (23 – 105) and 37.8 (11 – 80) during the nursing period. The mean number of pups born in the study area during the 2014 – 2015 breeding period was 86.1 individuals.

Response frequency was significantly correlated with the study area population (n= 184, Bandwidth= 21.88052, p= 0.0003; Figure 12a, Table 5) and the number of neighbours (n= 184, Bandwidth= 5956578, p <0.0001; Figure 12b, Table 5).

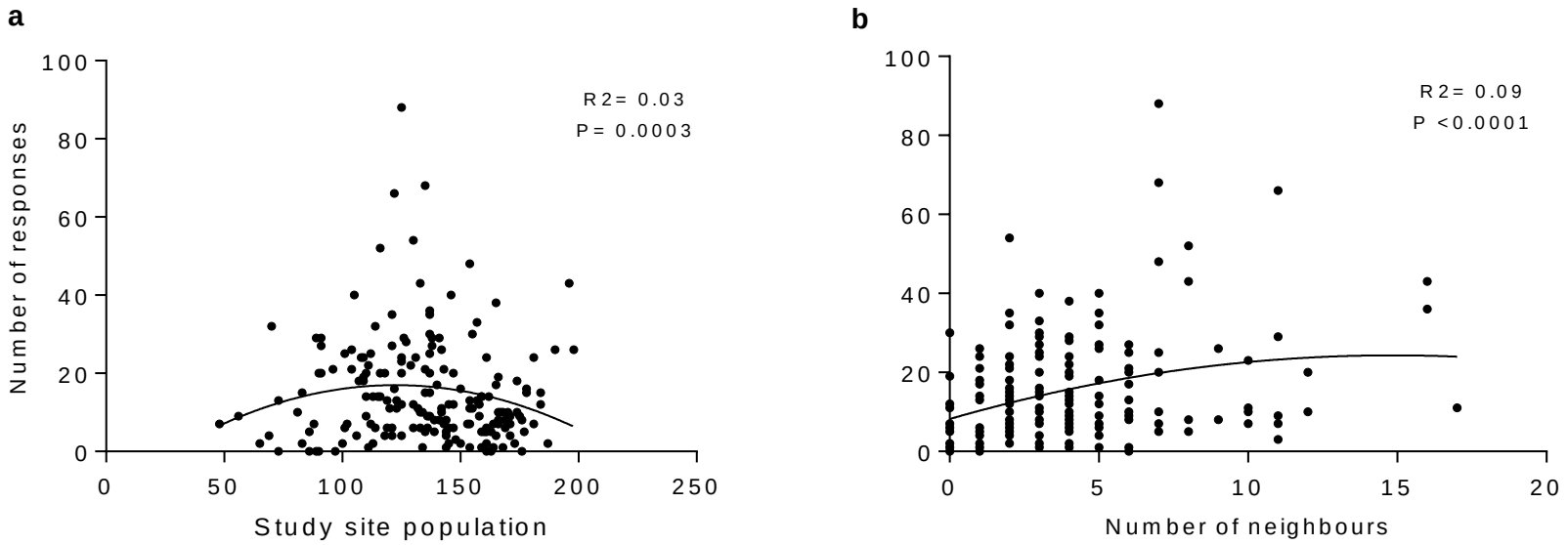

Figure 12. a. Number of focal female responses as a factor of study area population. **b.** Number of focal female responses as a factor of number of neighbours.

The proportion of aggression was the only predictor to significantly affect the response distance (n= 164, t= -2.423, p= 0.01; Figure 13, Table 6). None of the biotic variables were found to significantly affect the average aggression distance (Table 7).
The proportion of aggression was found to be significantly influenced by the number of encounters (n= 176, Bandwidth= 8.076742, P= 0.03; Figure 14a, Table 8) and the number of female neighbours (n= 176, Bandwidth= 13165653, P= 0.02; Figure 14b, Table 8).

The female population within the study area was significantly larger during the birthing period than during the nursing period (n= 184, W= 4037.5, p <0.0001; Figure 15a). The number of female neighbours was also significantly higher during the birthing period (n= 184, W= 3045, p= 0.001; Figure 15b). However, neither the number of encounters with females (n= 184, W= 2470, p= 0.393), nor the proportion of aggression (n= 133, W= 1505, p= 0.149) towards approaching females differed significantly between the birthing and the nursing periods.

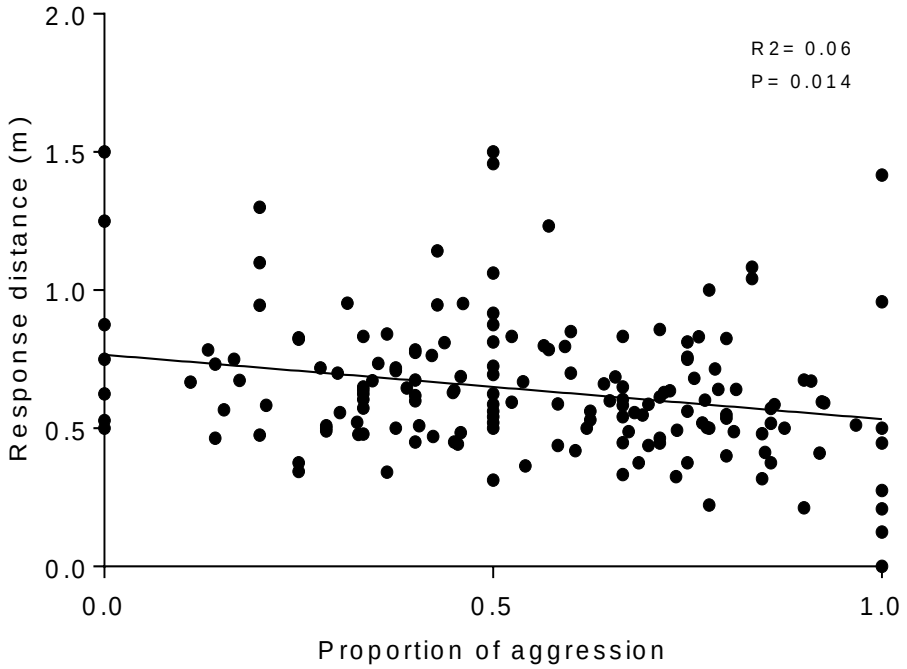

Figure 13. Focal females' response distance (m) as a factor of proportion of focal female aggression.

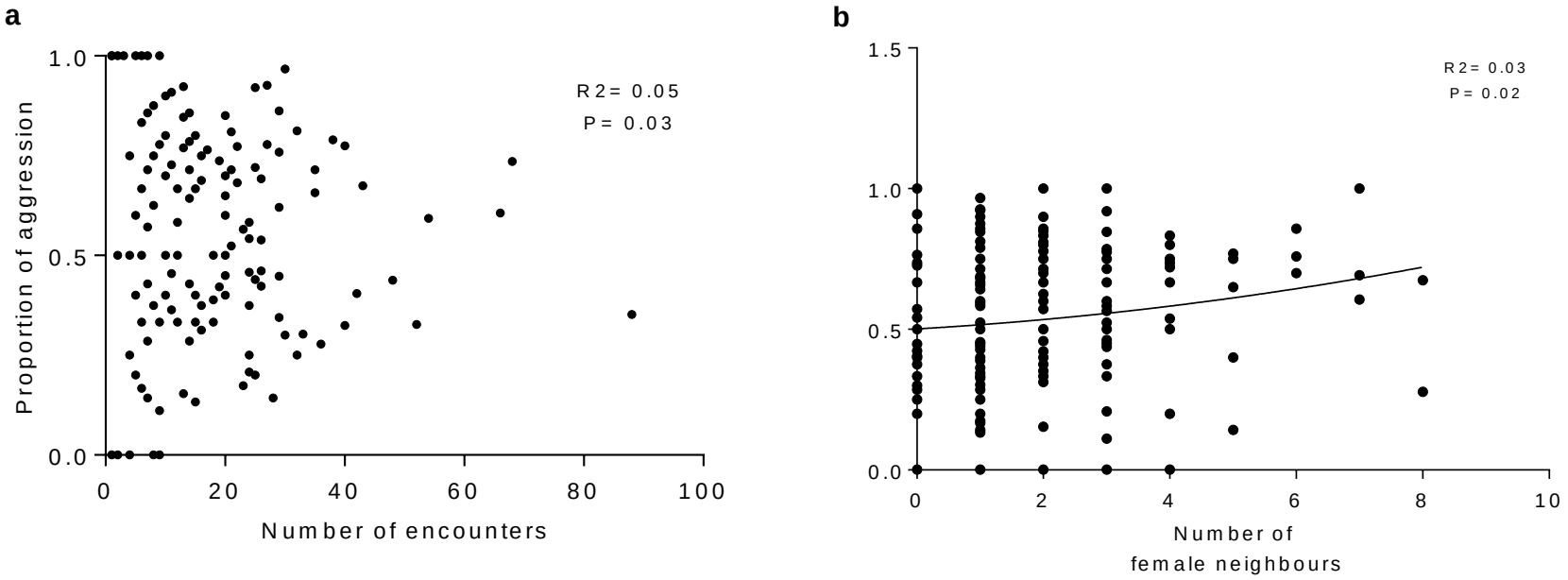

Figure 14. Proportion of focal female aggression as a factor of **a.** number of encounters with conspecifics, **b.** number of female neighbours of focal females.

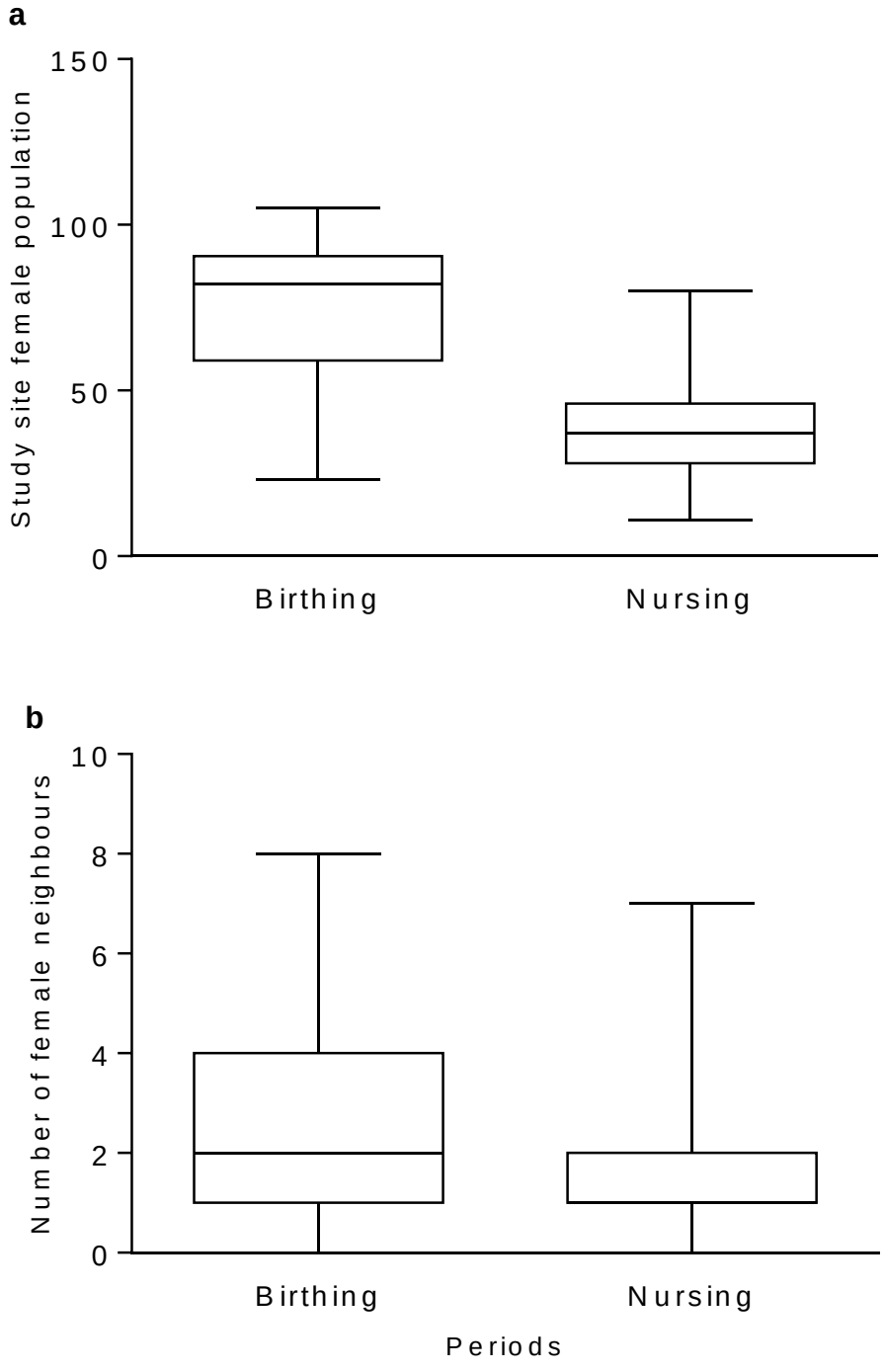

Figure 15. a. Comparison of the study site female population between the birthing and nursing periods**. b.** Comparison of number of female neighbours of focal females between the birthing and nursing periods.

Presence of dominant males

During the breeding phase observed over the study period (24 November – 7 January), the number of males defending an established territory in the study area ranged from 5 to 13. There were no significant relationships between the response distances of focal females towards all opponents with the number of dominant males present in the study area (n= 164, t(162)= 1.819, p= 0.07), or between the aggression distance of focal females towards approaching seals with the number of dominant males in the study area (n=165, t(163)= 0.508, p= 0.6). There was also no significant relationship between the proportion of aggression and the number of dominant males in the colony (n= 176, bandwidth= 0.5114216, p= 0.6).

There were no significant differences in the response distances of focal females towards all approaching seals, between the presence and absence of a male neighbour (within a 2 m radius) (n= 164, t(162), p= 0.206), or in the aggression distance of focal females between the presence and absence of a male neighbour (n= 165, t(163)= 0.991, p= 0.162). There was also no significant difference in the proportion of aggression between the presence and absence of a dominant male in the vicinity of the focal females (n= 176, W= 1638.5, p= 0.6).

Neither the number of female neighbours (n= 184, Bandwidth= 1.782255, p= 0.53) nor the nearest-female neighbour distance (n= 145, Bandwidth= 1.690599, p= 0.35) were significantly influenced by the presence of males. The presence and absence of a male neighbour did not significantly influence the number of female neighbours (n= 184, W= 2277, p= 0.13) or the nearest-female neighbour distance (n= 145, W= 1184, p= 0.8).

Neighbour density and distance

The mean number of focal females' neighbours (individuals within 2 m radius of the focal female) for each demographic were: adult males- 0.13 (range 0 – 1), adult females- 1.9 (0 – 8), pups- 2 (0 – 16).

The mean distances between the focal female and neighbouring demographic were: adult males- 1.3 m ± 0.12 (± SE), adult females- 1.05 m ± 0.03 and pups- 1 m ± 0.03.

Although the distance of neighbouring pups from the focal female was not significantly influenced by the aggression distance of the focal female, the number of pups significantly declined with increasing aggression distance (n= 165, Bandwidth= 682698.9, p= 0.002; Figure 16, Table 9). Neither the numbers of adult males or females in the vicinity of the focal female were significantly affected (Table 9). None of the mean distance of focal females from different neighbouring demographics was significantly influenced by the aggression distance (Table 9).

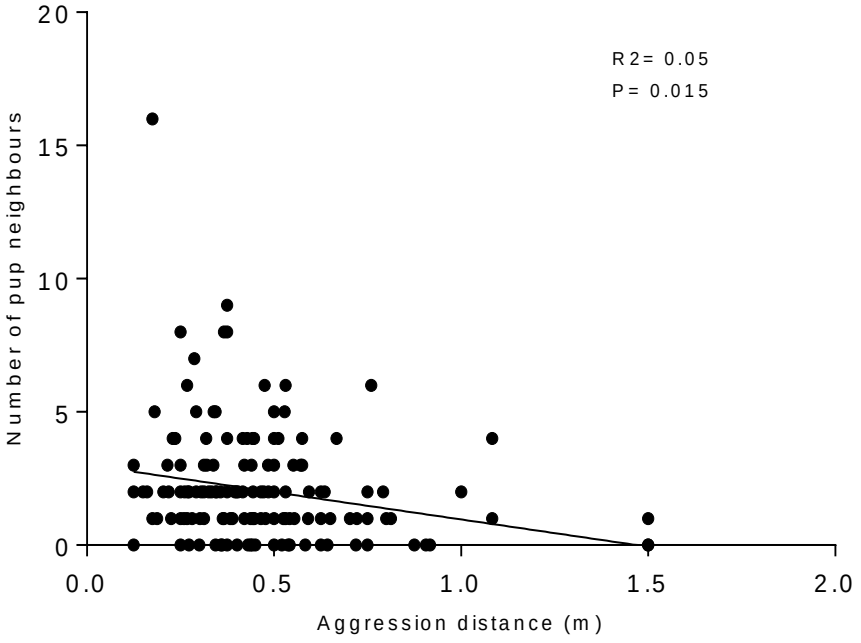

Figure 16. Number of focal females' pup neighbours as a factor of focal females' aggression distance (m).

The proportion of aggression of the focal female was also found to increase in response to an increase in the number of female neighbours (n= 176, Bandwidth= 4529969, p= 0.035; Figure 17, Table 11).

An increase in the focal females' proportion of aggression was found to significantly increase the distance of male neighbours from the focal female (n= 22, Bandwidth= 0.1977621, p= 0.028; Figure 18a; Table 10), while having no significant effect on either the mean distance from neighbouring females or pups (Table 10). The number of female neighbours was found to significantly increase with an increase in the proportion of aggression (n= 176, Bandwidth= 0.1180071, p= 0.032; Figure 18b; Table 10), but the number of male and pup neighbours were uninfluenced (Table 10).

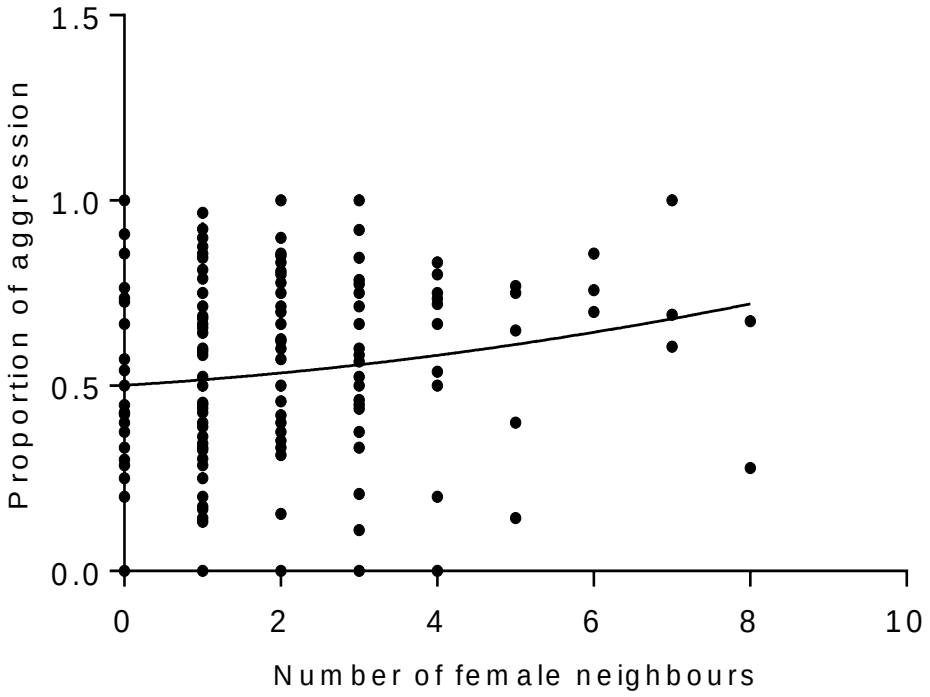

Figure 17. Proportion of aggression as a factor of number of female neighbours.

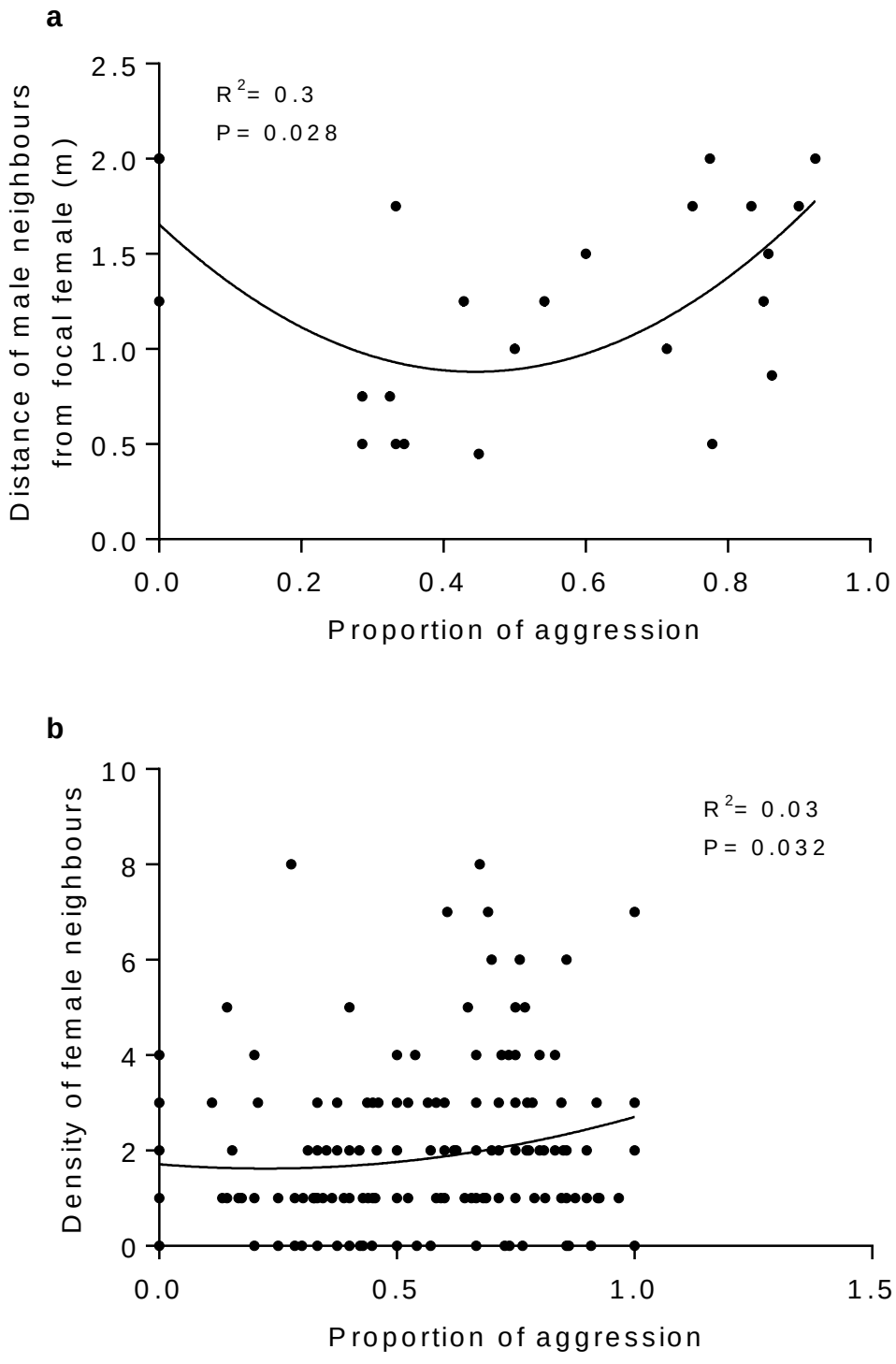

Figure 18.a. Distance of neighbouring males from focal female (m) as a factor of proportion of focal female aggression. **b.** Number of neighouring females from focal female as a factor of proportion of focal female aggression.

Presence and absence of filial pup

Pup births were recorded from the beginning of the study period 24 November 2014 to 28 December 2014. The median date of birth was 11 December 2014.

The response distance of focal females towards seals of all ages and sex was significantly longer when the focal female's offspring was present, in comparison to when their offspring was absent (n= 94, t(92)= 2.07, p= 0.02; Figure 19a). Similarly, the aggression distance was significantly longer when the offspring of the focal female was present (n= 88, W= 1240.5, p= 0.02; Figure 19b). However, there was no significant difference in the proportion of aggression between the presence and absence of the focal offspring (n= 19, t(36)= 0.2, p= 0.4).

The response distance of focal females towards adult females in the presence of the focal females offspring did not differ in comparison to when the offspring was absent (n= 34, t(32)= 1.064, p= 0.15; Figure 20a). The aggression distance of focal females towards adult females in the presence of the focal females offspring showed a marginally non-significant difference in comparison to when the offspring was absent (n= 22, t(20)= 1.65, p=0.06; Figure 20b). This weak relationship is likely to have been caused by the small sample size, as out of all focal females whose encounter with other females occurred during both the presence and absence of their pups, the number of encounters with other females was low. The aggression distance towards approaching females in presence of filial offspring was 0.52m ± 0.2, while in absence of filial offspring it was 0.38 ± 0.2.

The focal female's response distance towards nonfilial pups did not significantly differ between the presence and absence of its filial pup (n= 72, t(70)= 0.944, p= 0.17; Figure 21a). Similarly, the focal females' aggression distance towards nonfilial pups was not significantly different when filial pups were present or absent (n= 54, t(52)= 1.59, p= 0.06; Figure 21b).

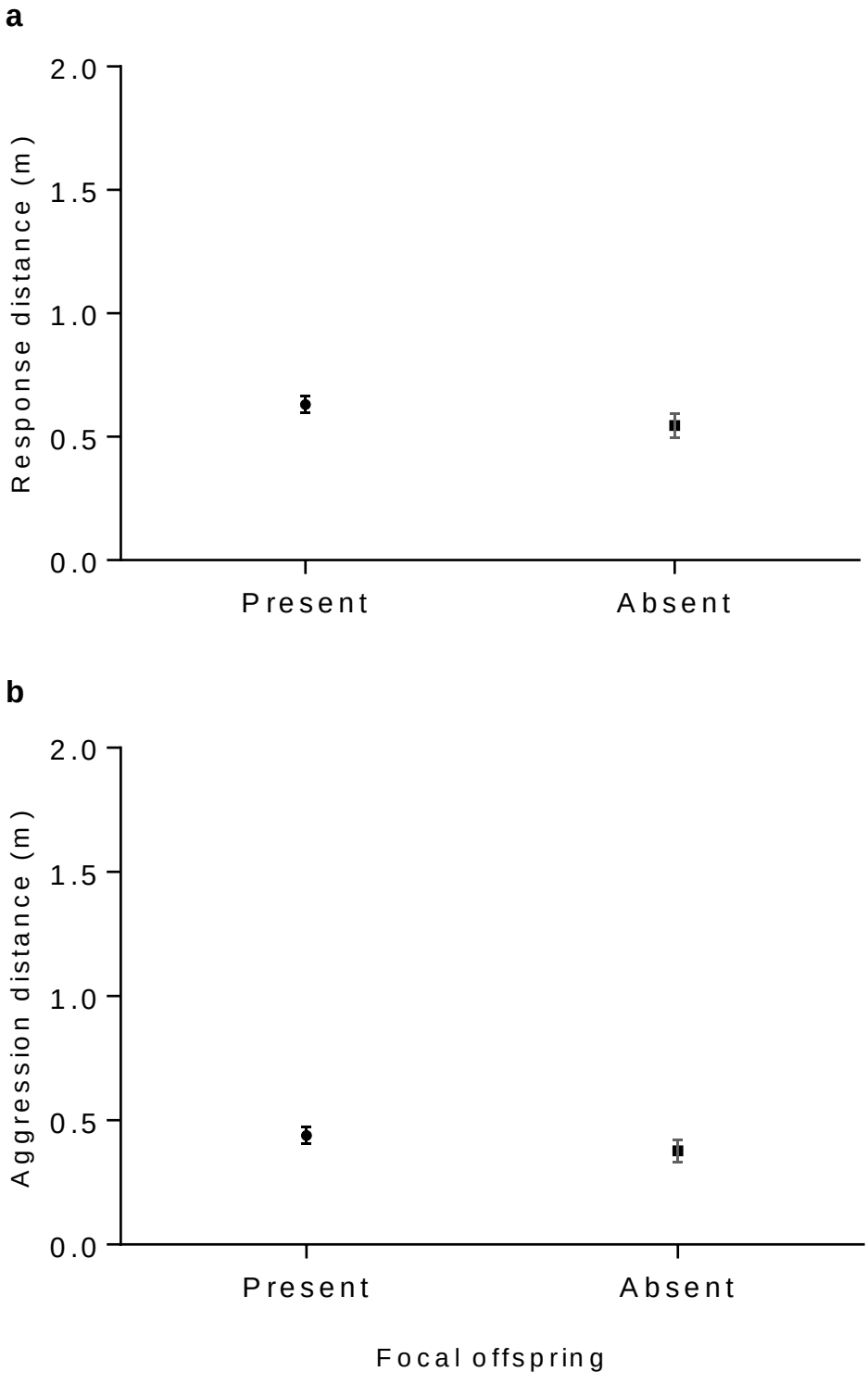

Figure 19. a. Focal females' response distance (m) towards all opponents compared between the presence and absence of the focal offspring (mean and standard error bars). **b**. Focal females' aggression distance (m) towards all opponents compared between the presence and absence of the focal offspring.

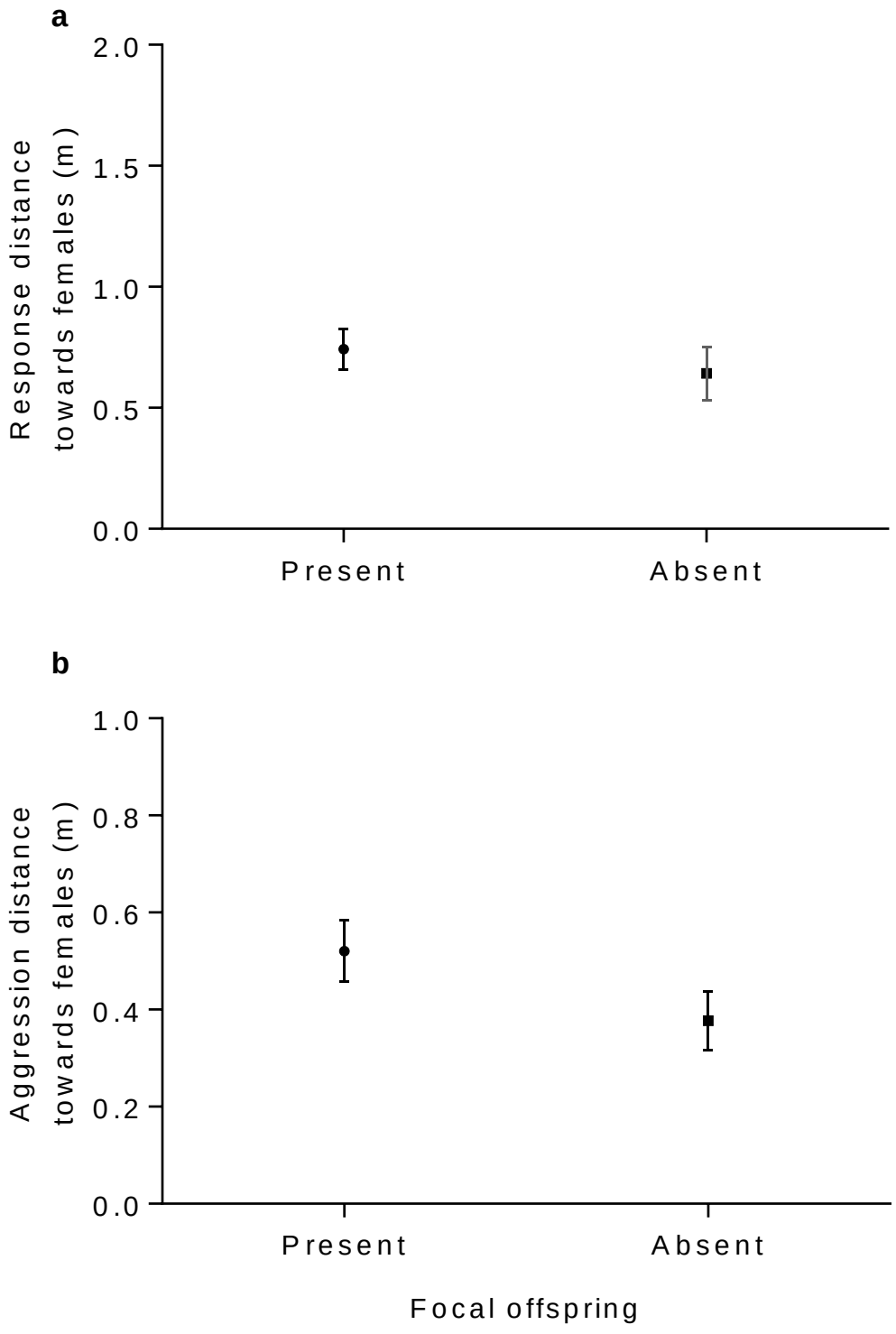

Figure 20. a. Focal females' response distance (m) towards female opponents compared between presence and absence of focal offspring, (mean and standard error bars). **b**. Focal females' aggression distance (m) towards female opponents compared between presence and absence of focal offspring.

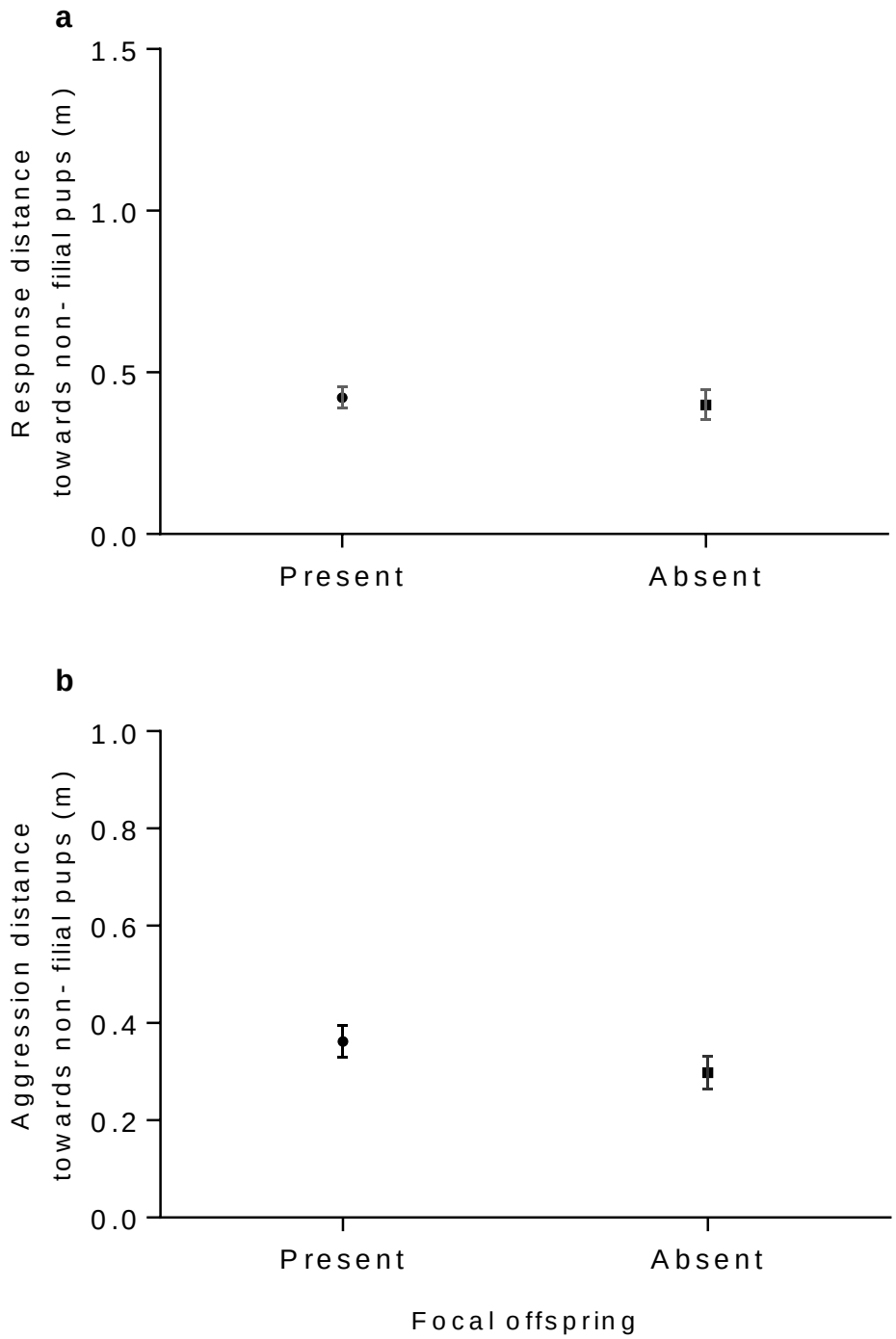

Figure 21. a. Focal females' response distance (m) towards non- filial pups compared between presence and absence of focal offspring (mean and standard error bars). **b.** Focal females' aggression distance (m) towards non- filial pups compared between presence and absence of focal offspring.

Focal female locations

The distance from the focal females' location from the sea significantly decreased with increasing rock temperature (n= 121, t= -2.932, p= 0.004; Figure 22a), as it did with the distance from the nearest pool (n=121, t= -3.629, p= 0.0004; Figure 22b).

Neither the distance from the sea nor distance from the nearest pool from of focal female locations were significantly affected by the time of day (Table 12). This suggests that the strong relationship shown between the distance from the sea and the distance from the nearest pool from the focal areas with the rock temperature was most likely due to the temperature differences, and not by the time of day, which may influence the location of seals arriving and leaving the colony to feed.

The total number of focal females' neighbours was significantly influenced by the distance from the sea (n= 131, Bandwidth= 11.129, p= 0.02; Figure 23a, Table 13) and the distance from the nearest pool (n= 131, Bandwidth= 24339572, p= 0.03; Figure 23b, Table 13). The number of neighbours was also significantly influenced by the size of rock of the focal female location (n= 128, H(4)= 19.139, p= 0.0007; Figure 23c, Table 13). The number of female neighbours was weakly influenced by the focal female location's distance from the sea (n= 131, Bandwidth= 90781309, p= 0.055; Table 13), while it was significantly influenced by the distance from the nearest pool (n= 131, Bandwidth= 245019066, p= 0.015; Figure 24a, Table 13) and the rock size (n= 128, H(4)= 11.726, p= 0.02; Figure 24b, Table 13).

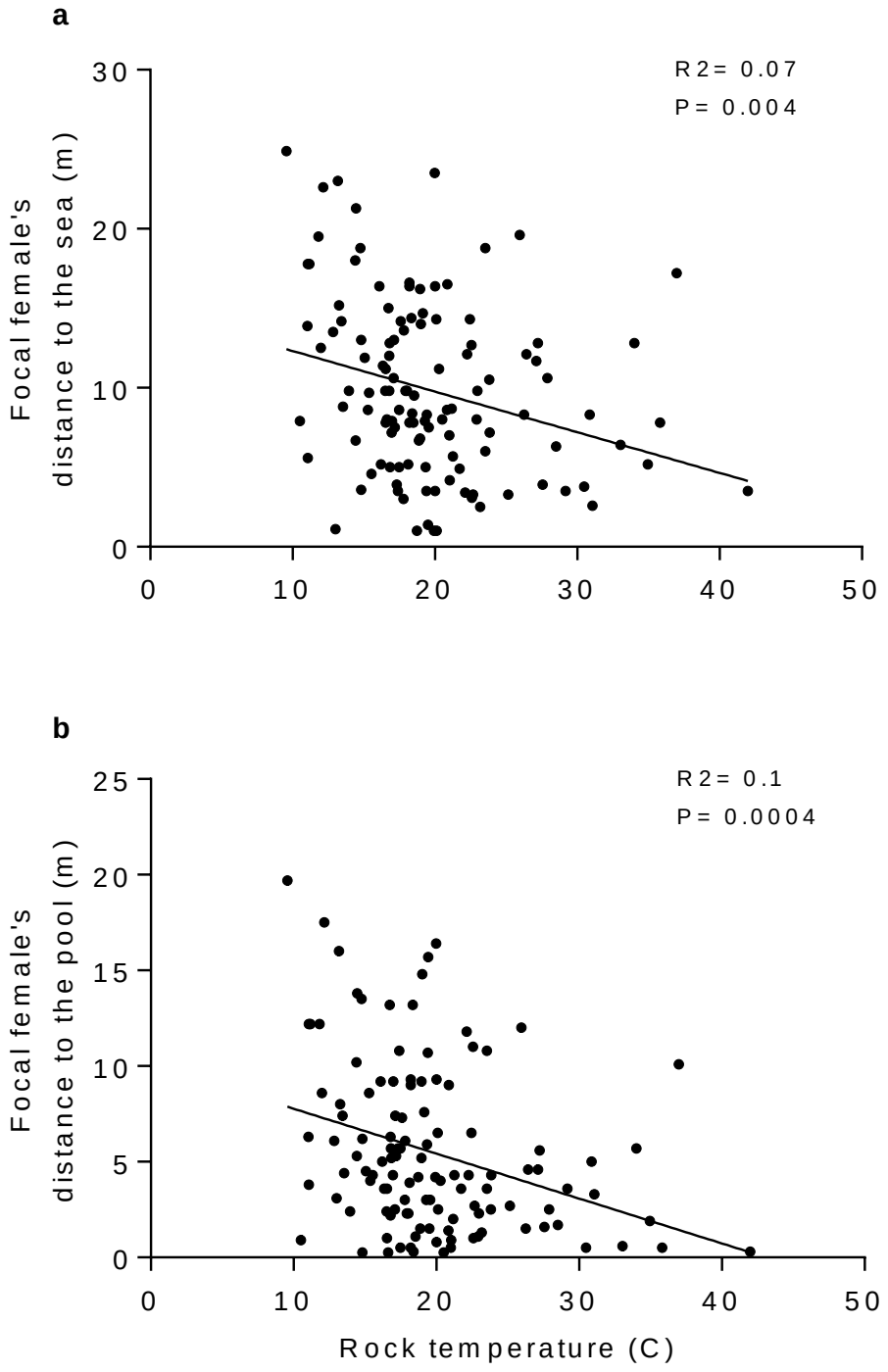

Figure 22. a. Focal female locations' distance from the sea (m) as a factor of rock temperature. **b.** Focal female locations' distance from the nearest pool (m) as a factor of rock temperature.

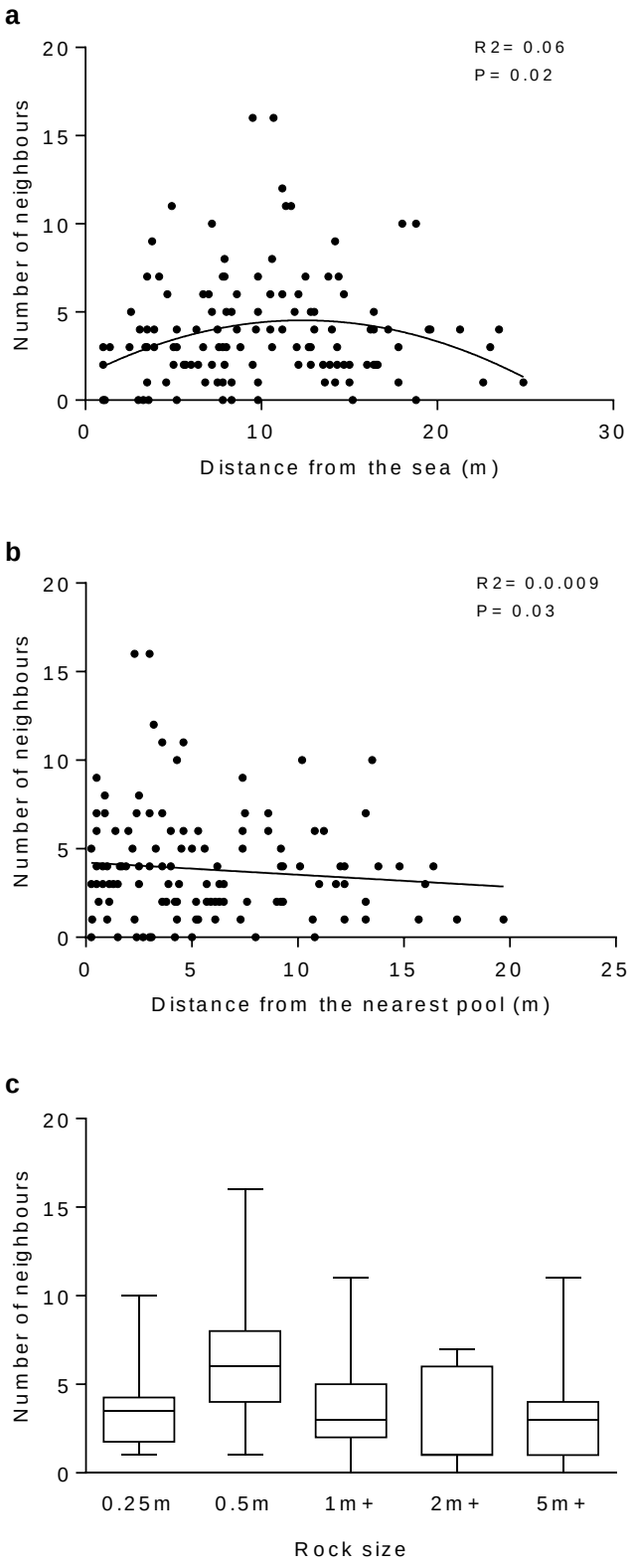

Figure 23. a. Number of neighbours of focal females as a factor of focal female locations' distance from the sea (m). **b.** Number of neighbours of focal females as a factor of focal female locations' distance from the nearest pool (m). **c.** Number of neighbours of focal females compared between rock sizes of focal female location.

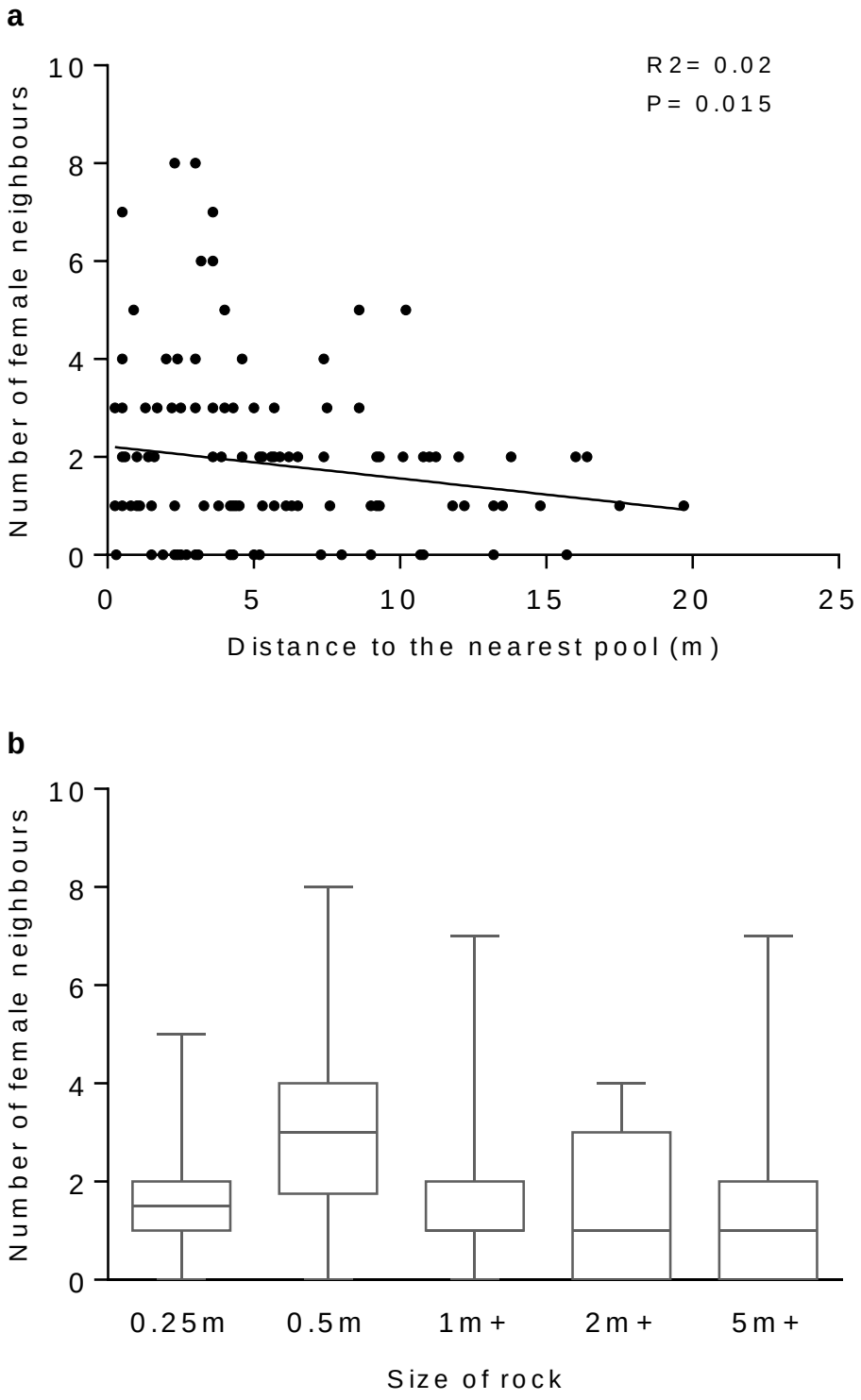

Figure 24. a. Number of female neighbours of focal females as a factor of distance to the nearest pool (m). **b.** Number of female neighbours of focal females compared between rock sizes of focal female location.

The distance of the focal females' areas from the sea and the nearest pool, and the size of the rock at the focal females' areas did not significantly influence the response distance, aggression distance or the proportion of aggression of the focal female (Table 14).

However, I hypothesized that if focal females actively defended sites of higher perceived quality, the aggression should significantly differ with the focal female location within each of the birthing and nursing periods. Aggression proportion significantly decreased with increasing distance from the sea (n= 22, Bandwidth= 104709980, p< 0.0001; Figure 25a, Table 15) and the nearest pool (n= 22, Bandwidth= 163066350, p= 0.018; Figure 25b, Table 15) during the birthing period (Table 15), but not during the nursing period (Table 15). Response distance and aggression distance were not influenced by the distance from the sea or the nearest pool in either of the breeding periods (Table 15, Table 16).
To explore the possibility of the higher aggression proportion in areas nearer the sea and the pool during the birthing period having been influenced by the higher density in these areas (Table 13), I tested the number of encounters during the birthing period. The number of encounters was not significantly influenced by the distance from the sea or the nearest pool (Table 15).

The focal female location's distance from the sea was significantly longer in the presence of higher number of males in the study area (n= 131, t= 2.578, p= 0.011; Figure 26a, Table 17). The rock size of the focal female locations was also significantly affected by the number of males in the rookery (n= 128, t(4)= -4.408, p <0.0001; Figure 26b, Table 17). The distance from the pool was not affected by the number of males (Table 17).
The distance from the sea, the nearest pool, and the size of the rocks were not significantly influenced by the number of males in the rookery during the nursing period (Table 17).

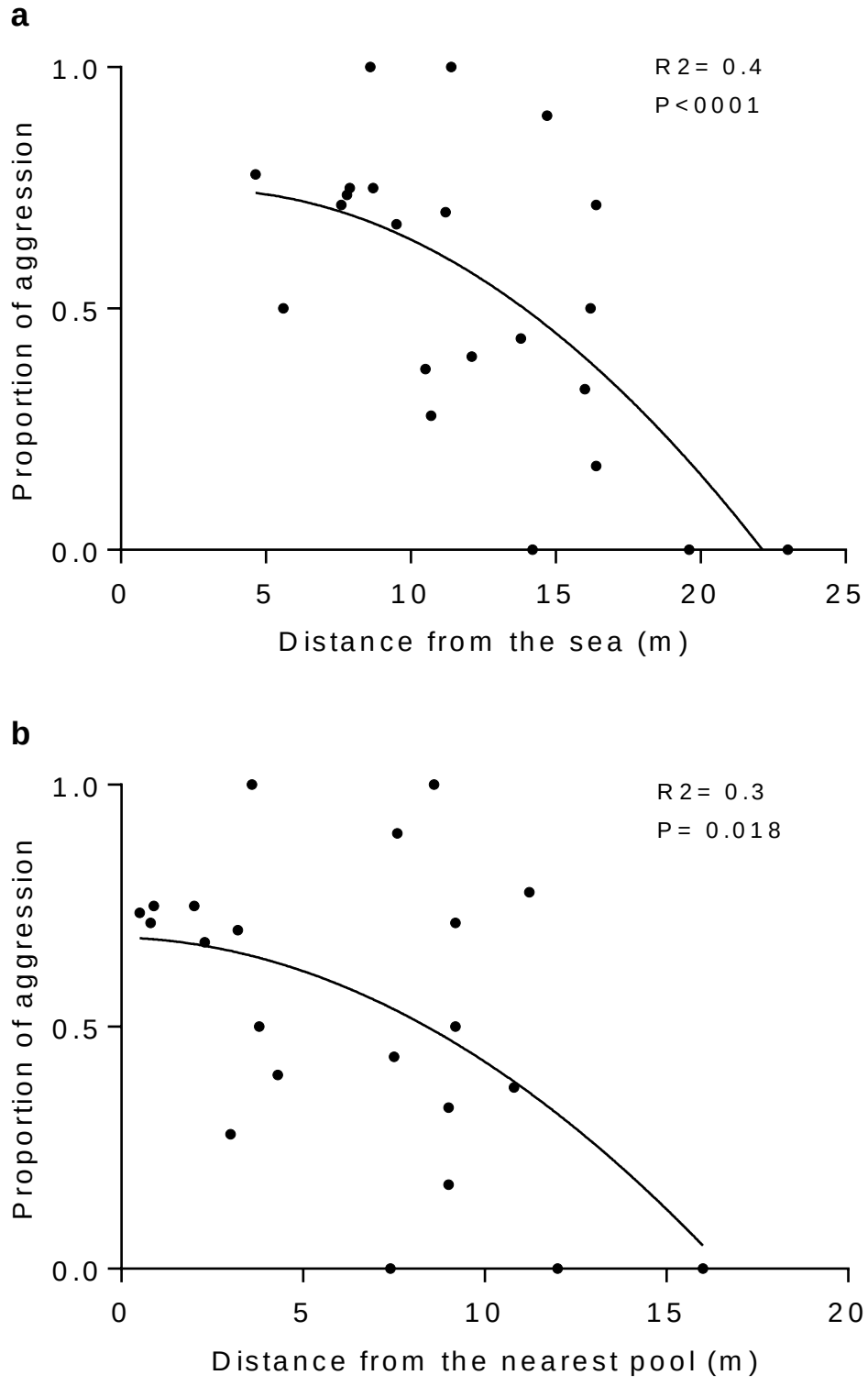

Figure 25. a. Proportion of focal female aggression during birthing period as a factor of the focal female location's distance from the sea (m). **b.** Proportion of focal female aggression during the birthing period as a factor of the focal female location's distance from the pool (m).

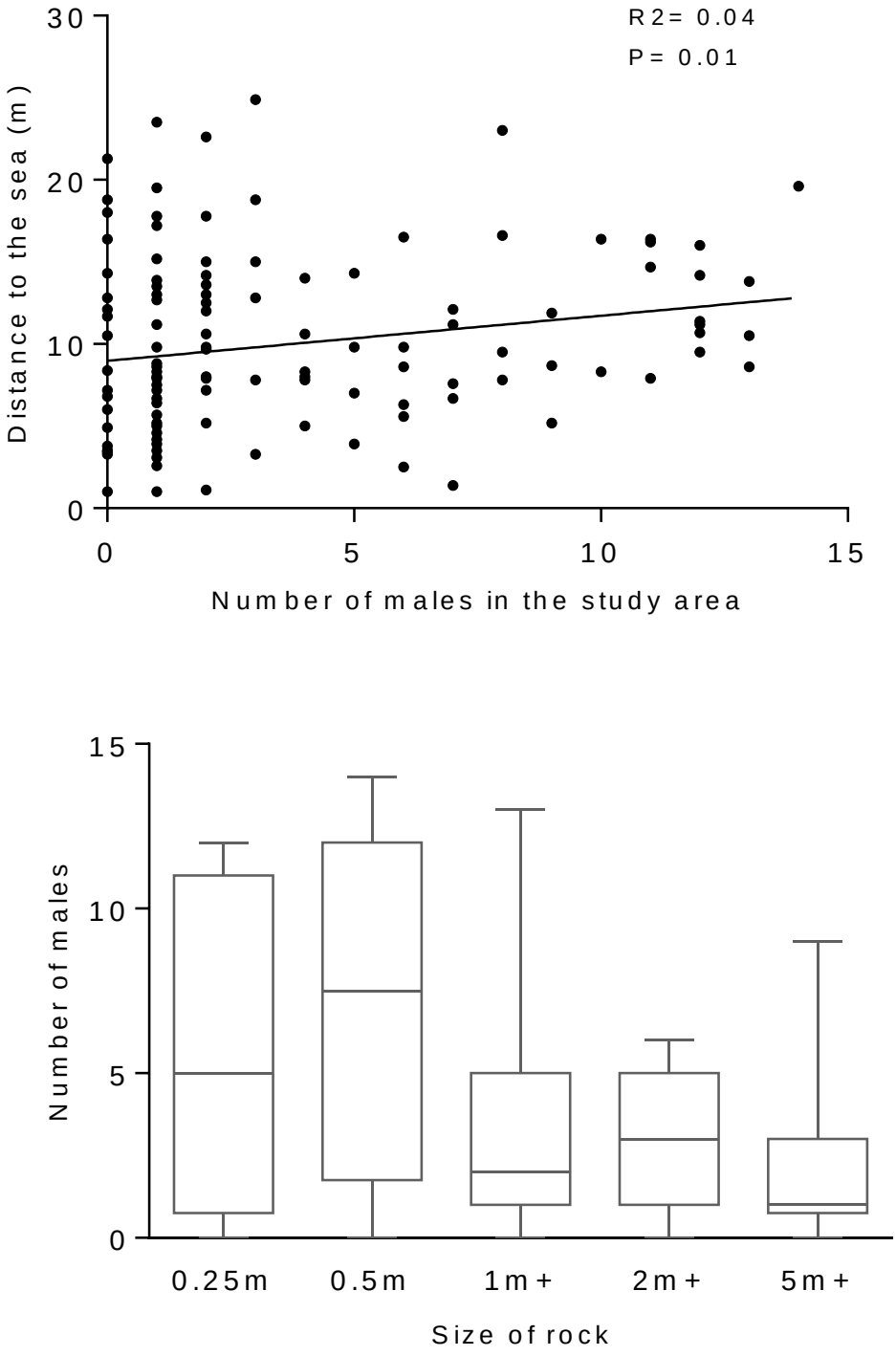

Figure 26. a. Focal female location's distance from the sea (m) as a factor of number of males in study area. **b.** Comparison of number of males in study area between various sizes of rocks of focal female locations.

During the birthing period, 97% of the focal females were observed only in one portion, of approximately 475 m^2, of the breeding colony. This area was solely composed of rocks and boulders sized approximately 0.25 m to 2 m. During the nursing period, the focal females were dispersed over the entire breeding colony of approximately 1155.46 m^2, on a range of rocks sized approx. 0.25m to >5 m.

The distance from the focal female location from the sea (n= 131, t(129)= 2.43, p= 0.04; Figure 27a), the closest pool (n= 131, t(129)= 1.72, p= 0.008; Figure 27b), and also the focal female location's rock size n= 128, W= 365, p= 0.0001; Figure 27c) significantly differed between the birthing period and nursing period. The rock size group of >5 meters was excluded, to eliminate bias.

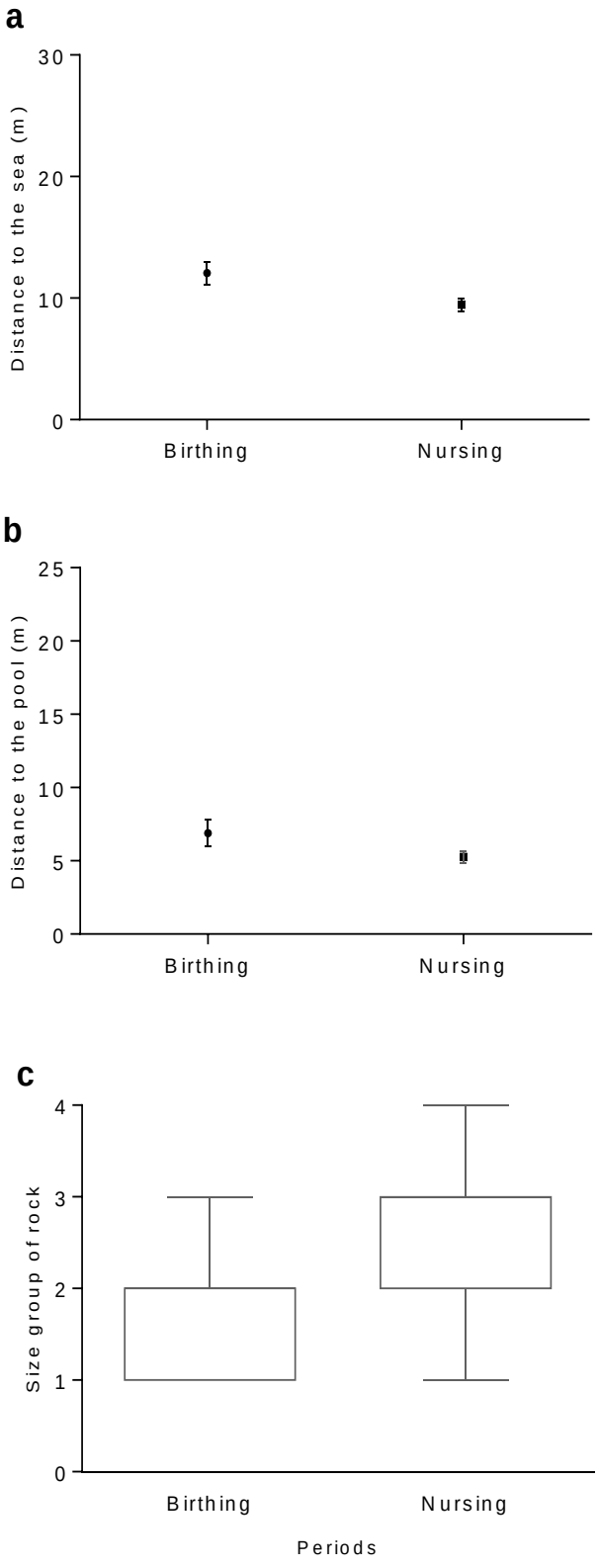

Figure 27. a. Comparison of the focal female locations' distance from the sea (m) between birthing and nursing periods. **b.** Comparison of the focal female locations' distance from the nearest pool (m) between birthing and nursing periods. **c.** Comparison of the size of rocks of focal female locations between birthing and nursing periods (Size group guide: 1- 0.25 m, 2- 0.5 m, 3- 1 m, 4- 2 m).

Nearest female neighbour distance

The distance to the nearest female neighbour significantly decreased with increasing rock temperature (n= 136, t= -2.114, p= 0.035; Figure 28a, Table 18) and was significantly lower during midday (n= 146, H(2)= 10.0651, p= 0.007; Figure 28b, Table 18). No other environmental predictors had a significant effect (Table 18.).

The distance to the nearest female neighbour significantly decreased as the number of neighbours (n= 146, t= -2.681, p= 0.007; Figure 29a, Table 18) and the number of female neighbours increased (n= 146, t= -5.681, p< 0.0001; Figure 29b, Table 18). The distance to the nearest female neighbour also significantly in-decreased with increasing response distance (n= 143, t= 2.342, p= 0.019; Figure 30a, Table 18), but the aggression distance did not have a significant effect (Table 18). The distance to the nearest female neighbour significantly decreased with an increase in the distance of the focal female location to the nearest pool (n= 101, t= 2.379, p= 0.017; Figure 30b, Table 19), while being unaffected by the distance to the sea or the size of the rock (Table 19).

The mean nearest female neighbour distance did not significantly differ between the birthing and the nursing periods (n= 101, W= 1339, p= 0.276).

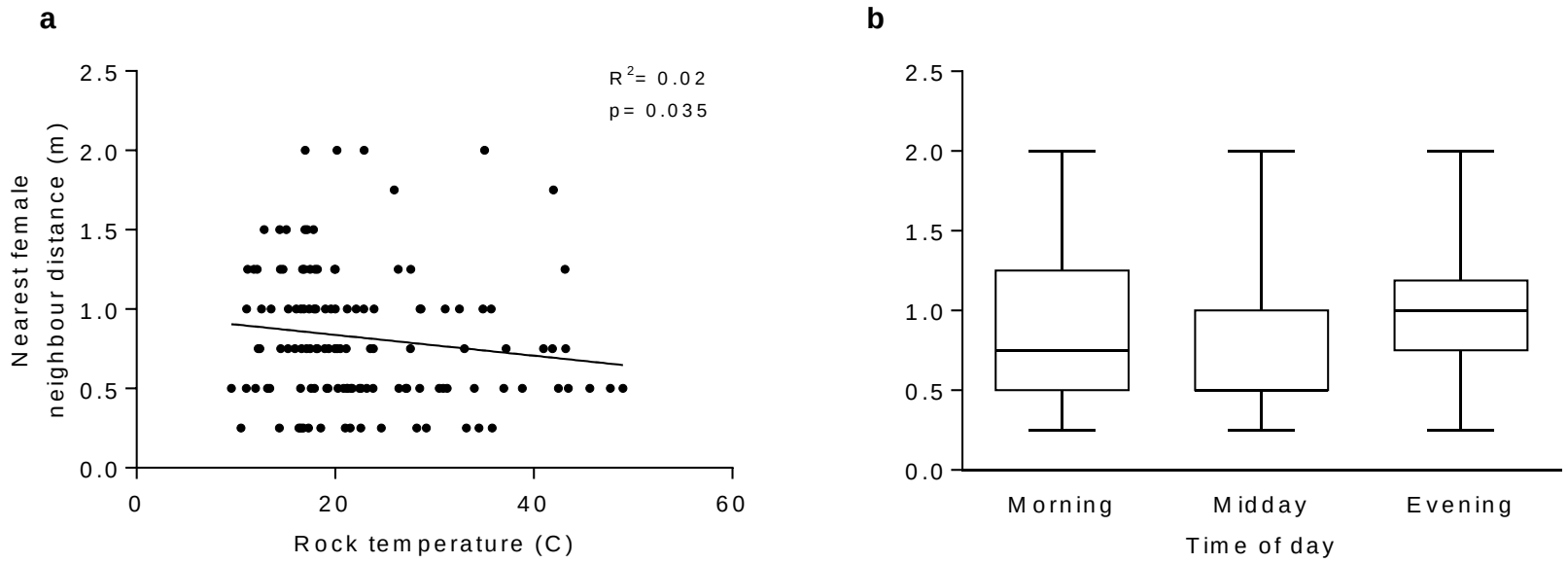

Figure 28. a. Nearest- female neighbour distance (m) as a factor of rock temperature. **b.** Nearest female neighbour distance (m) as a factor of time of day.

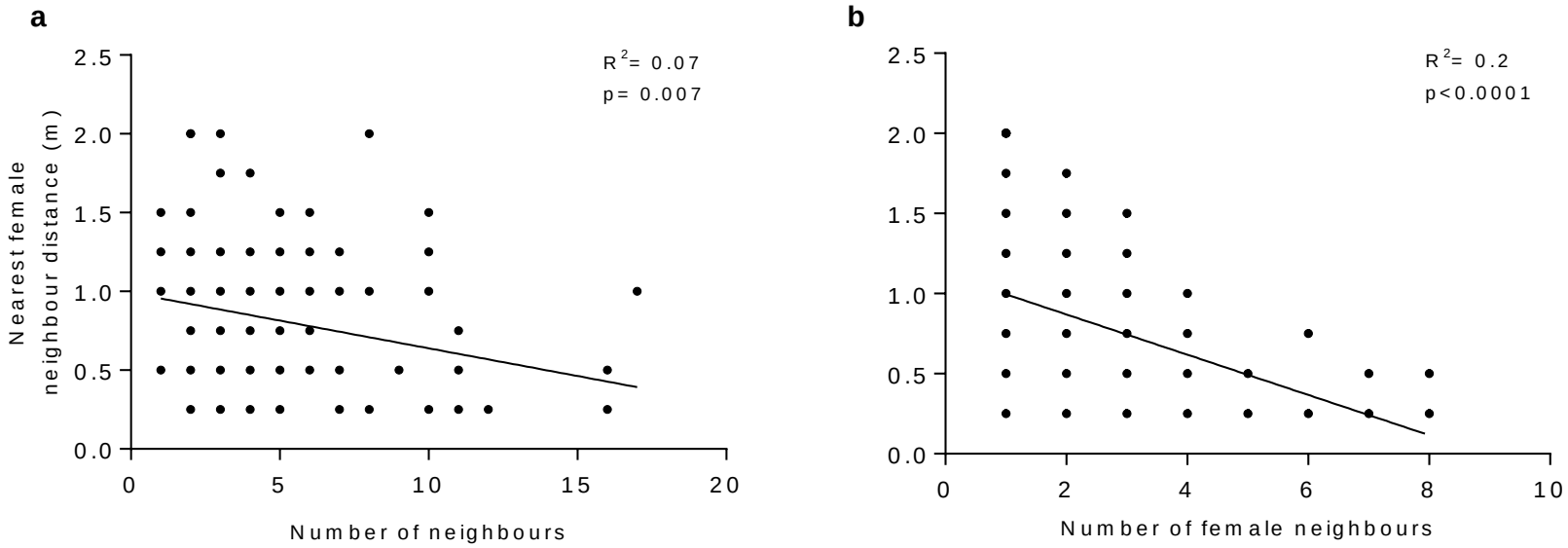

Figure 29. Nearest-female neighbour distance (m) as a factor of **a.** number of neighbours of focal females, **b.** number of female neighbours of focal females.

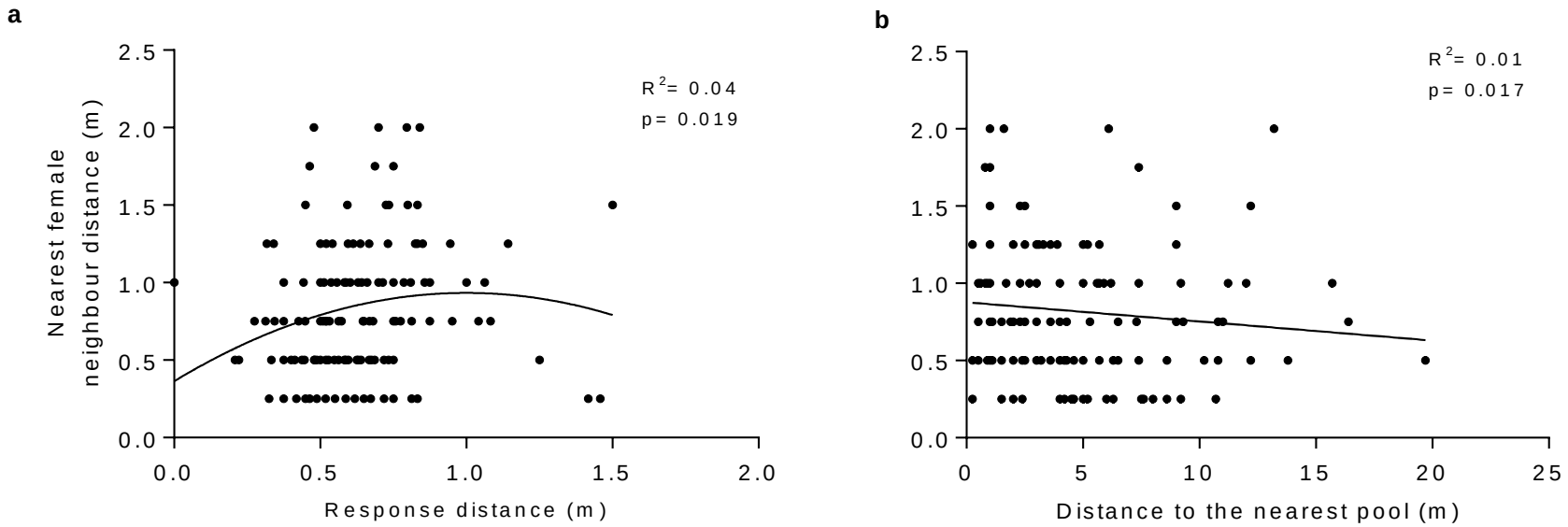

Figure 30. Nearest-female neighbour distance (m) as a factor of **a.** focal females' response distance (m), **b.** focal female locations' distance to the nearest pool (m).

Rookery carrying capacity

The aggression distance was 0.46 ± 0.05 m during the birthing period and 0.45 ± 0.02 m during the nursing period. The mean nearest female neighbour distance was 0.76 ± 0.09 m during the birthing period and 0.84 ± 0.04 m during the nursing period.

The period of the breeding season significantly influenced the predicted breeding female carrying capacity in the study area, due to the large difference between the area sizes inferred from site usage by females during each of these periods. The predicted carrying capacity within the study area using the aggression distance was 303.55 individuals for the birthing period and 750.79 individuals for the nursing period; the prediction using the nearest neighbour distance during the birthing period was 195.33, while it was 428 individuals for the nursing period, showing a huge difference between each method of dispersion measurement and also between the different periods (Table 20).

Discussion

A number of measures of female aggression which have not been commonly used in the studies of pinniped behaviour were employed in this research, to investigate the function of female aggression, its effects on female dispersion and the spatial population dynamics of the Ohau Point population of the New Zealand fur seal. As hypothesized, the functions of female aggression in the New Zealand fur seal appear to vary from those of the other pinniped species, presumably due to the disparity in social behaviour and reproductive ecology between these species. In contrast to the original hypothesis, it was found that the inter-female aggression was not the primary mediator of female dispersion.

Conspecific female aggression in the study population

This research on a subset of the Ohau Point New Zealand fur seal breeding colony has observed female aggression towards conspecifics of all ages and sex to be a common occurrence. Females are the numerically dominant sex in the resident adult population in rookeries during the breeding and pup rearing periods (Stirling 1971; Miller 1975; Goldsworthy & Shaughnessy 1994; Harcourt 2001; Boren 2005); therefore, female aggression is be expected to be the primary social factor to affect the spatial dynamics within a rookery. The female individual area size inferred from the nearest-female neighbour distance (or the individual distance) from this study, rather than the aggression distance (or the approach-tolerance distance), provides an indication of the degree of female influence on rookery dynamics, while the analyses of female aggression rate primarily assists in investigating the functions of female aggression.

The mean rate of inter-female aggression observed in this study population appears lower than for other fur seal species (c. 0.46 / 10 min). The total rate of focal female aggression in the Uruguayan population of Southern fur seal was 4.0 / 10 min, with inter-female rate of aggression at 2.3 / 10 min (Cassini 2001), while the rate of inter-female aggression in the Peruvian population was 3.6 / 10 min (Harcourt 1992b). The rate of inter-female aggression in the Northern fur seal was 1.86 to 2.0 / 10 min in a

focal female study (Francis 1987). In an study of the Northern elephant seals by Christenson and Le Boeuf (1978), high variations between rookeries were found, and also between years on the same rookeries (up to 40% difference between years, up to 35% difference between rookeries). The variances in the rate of aggression observed between the studies of the same species, but different populations, suggest that the difference is likely an effect of density or environmental variables, while the variances observed between different species is likely due to the differing functions of aggression. The significantly lower rate of aggression in these phocid species may be due to their limited terrestrial mobility and capital breeding system (nursing from body reserves) allowing potential agonistic interactions only with neighbouring females, while income breeding (foraging in between nursing) otariid females of superior mobility have a higher chance of interacting with more residents of the rookery.

Thermoregulation

Increasing rock temperature was found to significantly decrease both the mean response and aggression distance of focal female seals, suggesting that their tolerance to the approach of conspecifics is higher when hotter. This is in contrast to my original hypothesis, which predicted that higher temperatures would cause fur seals to respond more aggressively to approaching seals, to prevent thermal input from the body heat of other individuals (Campagna & Le Boeuf 1988). The shorter approach-tolerance distance during periods of higher temperature found in this current study may be a form of thermoregulatory behaviour, as they attempt to reduce overheating by minimizing activity levels (Bohórquez-Herrera *et al.* 2014). For example, elephant seals were observed to minimize movement during high temperature and humidity levels, possibly to limit overheating due to activity (Norris, Houser & Crocker 2010). Male New Zealand sea lions *(Phocartos hookeri)* were also observed to spend more time resting in summer, suggesting that thermoregulatory requirements limited activity at high temperatures (Beentjes 1989). Thermoregulatory resources such as pools and shade, and behavioural thermoregulation are necessary in California sea lions to reduce thermal stress (Matsuura & Whittow 1974). By reducing the approach-tolerance distance, New Zealand fur seal females may be attempting to minimize the number of aggressive encounters for thermoregulatory purposes. Thermal stress was frequently

observed in the focal females as various thermoregulatory behaviours were recorded such as flipper waving, visits to a pool or the sea, submerging hind-flippers in a pool and wetting of the hind-flippers with urine (Francis 1987; Campagna & Le Boeuf 1988; Wolf, Kauermann & Trillmich 2005). Mid-day was the hottest time of the day on average and the time in which the lowest number of females in the study area was recorded , even though New Zealand fur seals are known to haul out during the day and feed at night (Stirling 1968; Fea, Harcourt & Lalas 1999; Krajewski & Sazima 2010). This suggests that the absence of many females is likely due to leaving to the sea to cool down. Temperature as a significant influence on the number of seals on shore is also supported by a study of the diurnal movements of a non-breeding colony of the New Zealand fur seal by Stirling (1968), in which during spring and autumn, mid-day was the time of the day when the highest numbers of seals were recorded on the shore. New Zealand fur seals have previously been known to experience thermal stress, as air temperatures in New Zealand can exceed 30^{o}C (Mattlin 1978a). The highest rock temperature recorded in the current study exceeded 50^{o}C.

If females reduced aggression in response to high temperatures, we would expect to see decreased proportion of aggression. However, in this study, it was found that the proportion of aggression and the number of responses was greater with increase in rock temperature. Cassini (2001) also observed increased rate of aggression during periods of high activity, caused by an elevated number of visits to the water sources for thermoregulation during higher temperatures (Gentry 1973; Limberger *et al.* 1986; Francis & Boness 1991; Cassini 2001). The significantly higher number of responses of the focal females during hotter temperatures seen in this current study reflects this. This Increased female movement was also observed to increase the rate of female aggression in the northern fur seal, although the high movement during the evenings was likely due to departure for night foraging (Francis 1987). These results from past studies show that the number of aggression is mediated by the amount of movement of the seals in the rookery, but is not representative of whether females show more aggression per 100 interactions. As the current study showed the proportion of aggression to increase with rock temperature, it suggests that there is a higher potential for females to be aggressive during hotter temperatures.

Conversely, the results from a study on Californian sea lions (*Zalophus californianus*) observed fewer agonistic encounters at higher temperatures (Young *et al.* 2008). As sea lions are contact species allowing body contact with conspecifics, most fur seals are distance species; this may explain the difference in the aggression in relation to temperature between these species, as fur seals experience higher level of stress during periods of increased encounters with conspecifics. As female sea lions are more gregarious and tolerant of body contact, the higher proportion of aggression displayed by the New Zealand fur seals during warmer temperatures is likely to be a stress response due to the increased number of encounters, as they are forced to repel their conspecifics more often.

Many species of pinnipeds, especially fur seal species appear to be significantly affected by high temperatures on land due to their insulating layer of blubber and thick fur (Gentry 1973; Campagna & Le Boeuf 1988; Norris *et al.* 2010; Rosen & Trites 2013). Previous studies have recorded a number of distinct thermoregulatory behaviours in otariids to reduce overheating such as resting in the shade, submerging in water and flipper waving (Francis 1987; Wolf *et al.* 2005; Bohórquez-Herrera *et al.* 2014). As pinnipeds display a range of behaviours dedicated solely to thermoregulation, the higher tolerance to conspecific approach during hotter periods may also be a thermoregulatory behaviour. The vulnerability to overheating may also explain why pinnipeds display aggression in various intensities. Their initial ritualistic level of aggression (i.e. threat) towards approaching conspecifics may act as a warning of low energy expenditure to minimize movement and overheating, before the opponent approaches closer and results in a subsequent high-energy aggression (i.e. bite, neck-fight) (Bohórquez-Herrera *et al.* 2014). If this was the case we would expect to see the aggression of the highest intensity to be the most prevalent during low temperatures. However this study showed that the bite behaviour was the highest form of aggression shown during hotter temperatures. This prevalence of bites during higher temperatures is likely due to the shorter approach-tolerance distance, as shorter approach of opponents are increasingly tolerated, biting is more likely to occur. The decrease in the aggression distance and the prevalence of high intensity aggression during periods of high temperatures suggest that aggression of any intensity can cause overheating when

the temperature is high, and that there is no significant difference in the likelihood of overheating between threat and bite behaviours.
The lower aggression distance during hotter periods may also be explained by the increased frequency of encounters, as the seals may be attempting to reduce the number of aggressive encounters. Hazlett (1975) proposed that as density increased, individuals would be spending an increased amount of time in aggressive encounters, if their 'individual distance' (referred to as approach-tolerance distance in this current study) remained the same. Therefore, if the function of the reduced aggression distance was to minimize the amount of time spent in aggressive interactions, we would expect to see a reduced proportion of aggression with an increase in temperature. However, as aggression was found to significantly increase with temperature, it is likely that the decrease in the response and aggression distance during hotter temperatures was due to thermoregulatory stress.

In this study there was no correlation between female aggression distance and environmental factors such as cloud cover, tide level, wind speed and surf conditions, as was also seen in the northern fur seal (Francis 1987). In contrast, tide level and wind speed were seen to significantly increase the aggression levels of female elephant seals, as the females actively attempted to remain near their pups (Christenson & Le Boeuf 1978). Such difference could have arisen from the fact that mother-pup separations are more likely to result in fatal consequences in the elephant seals, than in fur seals, due to the inferior mother-pup recognition in the elephant seals (Insley 1992). This suggests that the difference in the mechanisms of maternal and social behaviour of otariids and phocids may be an indirect influence on the relationship between the aggression behaviour and external factors. Francis (1987) found that increasing wind speed resulted in a decrease the inter-female aggression in the California sea lion, although no relationship was observed with solar radiation, tide level, surf conditions or cloud cover (Francis 1987). However, unlike this study in which wind speed was estimated by the observer, Francis used an anemometer. The potential difference between the sea lion and the fur seal in regards to the influence of wind speed on the aggression behaviour may be explained by the coat thickness; the sea lion may experience increased loss of body heat with higher wind speeds due to their thinner pelage (Cassini 2000). This

suggests that even though wind speed can affect thermoregulation in some pinnipeds, it is not sufficient enough to alter the behaviour in the New Zealand fur seals.

Population density and dispersion

The results of this study show that the aggression distance of the focal females were not influenced by the biotic factors measured in this study. This suggests that the territory size of the female New Zealand fur seal is unlikely to be influenced by population traits such as study area density and local density, which may differ greatly between populations. Thus, female territory size inferred from this study may be applicable in assessing the density in other New Zealand fur seal rookeries, without the degree of female dispersion being influenced by the varying population traits between colonies.

In this study, the focal females were more likely to respond aggressively to approaching conspecifics with an increase in the number of female neighbours (seals within a 2 m radius of the focal female), but were unaffected by the number of females in the entire study area. However, as the female population of the study area was found to have a significant positive influence on the number of female neighbours, it can be suggested that the increase in the study area female population indirectly influenced the female aggression. Much of the past research on female aggression in other pinniped species has described a positive relationship between the rate of female aggression and female density of the rookery (Cassini & Fernández-Juricic 2003; Fernández-Juricic & Cassini 2007; Wolf & Trillmich 2007; Young *et al.* 2008). Positive relationships between aggression and density have also been found in other colonial species (Balbontín & Ferrer 2008). For example, conspecific aggression between breeding individuals was observed to be greater in high density colonies than low density colonies in the black-backed gull (*Larus marinus*) (Butler & Trivelpiece 1981). The positive influence of increasing local female density on aggression may be a reflection of the increased competition for space, or an increased effort to reduce the number of newly establishing females.

The mean aggression distance of focal females did not significantly affect the number of female neighbours, the mean distance from the neighbours to the focal female, or the nearest female neighbour distance. However, fact that the number of neighbouring pups was influenced by the female aggression distance suggests that aggression is able to act as a conspecific repellent. This suggests that although aggression distance has the capacity to cause changes in conspecific behaviour, it is unable to mediate the degree of female dispersion. The lack of influence that female aggression has on the degree of female dispersion leads me to propose that the anti-gregariousness in female adult New Zealand fur seals is more likely to be maintained by mutual avoidance, rather than active territorial behaviour. This distance between species mediated by both parties, instead of an one sided aggression, appears to be similar to the 'individual distance' proposed by Hediger (1950) (as cited by McBride 1971), described as the distance "measured during the resting subphase when it is a constant". There are also a number of traits in the behaviour and conspecific interaction in this species that contradict some basic definitions of territoriality, as outlined by Brown (1970). He outlines the definition of a territory as: "1. A fixed area, which may change slightly over a period of time, 2. Acts of territorial defence by the possessor which evoke escape and avoidance in rivals so that 3. The area becomes an exclusive area with respect to rivals." The defended areas of the female New Zealand fur seals are not fixed; they are highly mobile and frequently move around within the colony, and settling in different sites within a rookery to rest and nurse their pups is common. The aggressive defence of an area is only employed in the presence of approaching conspecifics, and females do not appear to make an effort to make themselves conspicuous to alert neighbours to their presence without provocation. Female fur seals also frequently leave any previously defended areas when departing for their foraging trips, which are readily taken and used by others in the absence of the previous occupants; this shows non-exclusivity of these areas. On the contrary, individual distance (or the individual area inferred from individual distance) has been described to move with the animal as it is not restricted to a specific geographical location (Conder 1949). Therefore, I propose that the dispersion of the female New Zealand fur seals of my study population is maintained by the individual distance, rather than the aggression distance.

Although the aggression distance was not found to influence the establishment decisions of female neighbours in relation to their distance from the focal female, higher proportion of aggression was found to positively correlate with the number of female neighbours. This opposes the theory that an increase in aggression in colonial individuals promotes higher rates of emigration and lower rates of immigration as previously proposed (Young *et al.* 2008) . According to this theory, one would expect a lower number of female neighbours around a female that displays more aggression; on the contrary, the findings of this study showed a higher number of females around a female that was more likely to be aggressive. As the number of females also had a significant effect on the proportion of aggression, it appears that either inter-female aggression asserts no negative influence on the neighbouring females, or that the strength of the positive effect of the number of female neighbours on the focal female is masking the negative effect of aggression on the female neighbours. Further study to quantify any potential influence of aggression on neighbouring females while controlling for the density-dependent effects on female aggression would be imperative in understanding the effects of aggression on the spatial population dynamics in colonial species.

Interestingly, the distance of the dominant males from the focal females was generally longer when the focal females were more likely to show aggression. This is surprising as males were observed to be uninfluenced by female aggression in past studies and this study. It could be hypothesized that this is an influence of longer distance from males facilitating higher amount of aggressive inter-female interactions, as they are less likely to attract attention from males that are further away. However, as this is unlikely, as the proportion of aggression did not increase with greater distance from the males. It appears that further research of the effect of female aggression on the males of the New Zealand fur seal is warranted.

The nearest female neighbour distance was significantly shorter at midday; this could be a result of the decreased aggression distance during the hotter time of the day allowing females to establish nearer the focal female. However, since the aggression distance was not found to have significant influences on the nearest female neighbour distance, it is likely that the shorter distance is due to the higher concentration of

females around a cooling resource such as a pool during the hotter time of the day. This is supported by the finding that the nearest female neighbour distance was significantly shorter when the focal female was near a tidal pool.

Influence of dominant males

One of the hypotheses was that the presence of dominant males in the colony may influence the response and aggression behaviour of adult female seals. Francis (1987) found Northern fur seals to congregate in higher densities than northern sea lions, as the fur seals attempted to avoid male harassment. In northern elephant seals, the increased movement from females attempting to avoid males searching for mating partners resulted in increased inter-female aggression levels (Christenson & Le Boeuf 1978). Also, in many pinniped species, injury from being trampled by males were observed to be a potential cause of fatality for pups, especially in rookeries of high density (McNab & Crawley 1975; Mattlin 1978b; Doidge *et al.* 1984). Therefore, as males can inflict harm on female health and reproductive fitness, female vigilance and level of aggression against males would be expected to increase, along with female density, in the presence of more males.

However, none of the female aggression, number of neighbours or the nearest-female neighbour distance was significantly influenced by the number of males or the presence and absence of male neighbours. Whilst past studies on numerous pinnipeds have shown a relationship between presence of males and female aggression (Christenson & Le Boeuf 1978), this does not seem to be the case in the NZ fur seal. This may be due to the fact that in contrast to other species such as the southern sea lion, male aggression of high intensity towards females or male-induced fatality in females appears to be virtually non-existent in the New Zealand fur seal. Initiation of aggression behaviour from dominant males towards females was not commonly observed over the entire study period and any aggressive behaviour displayed was of copulatory or defensive nature. Males commonly bite females during copulation; however, no injuries to the females were observed in this study or reported in previous studies on the New Zealand fur seal (e.g., Miller 1974). In this study, there was one observed instance of dominant male displaying a threat exaggeration towards a female, seemingly as a response to the

female biting an already-present wound on the hind area of the male. Males, especially the dominant males, were also observed to be highly tolerant of being bitten by females, and none of these interactions appeared to result in injuries to the males. This resulted in females being unable to effectively repel any approaching dominant males, and they were almost always displaced, especially if the male chose to occupy her resting spot. The considerably low risk of male-inflicted injury to females in the New Zealand fur seals is possibly the main reason that the effect of male presence on females' response and aggression toward them is relatively insignificant in this species. Such variance in the behaviour of females among species shows that male behaviour can alter the aggression behaviour of females to varying degrees.

Male 'peacekeeping' behaviour is commonly seen in otariids, in which the inter-female aggression results in dominant males approaching and interrupting the fight (Miller 1974; Fernández-Juricic & Cassini 2007; Bohórquez-Herrera *et al.* 2014). Males are thought to display this behaviour to minimize the loss of females in their territory or harem induced from inter-female aggression, and to prevent the females from mating with neighbouring males that may have also been attracted to the commotion (Fernández-Juricic & Cassini 2007). In the Northern elephant seal, female aggression towards males attract neighbouring males, resulting in a competition between the males, from which the winner mates with the female (Cox & Le Boeuf 1977). Investigation by dominant males of inter-female aggression and female aggression towards intruder males in their territory were both observed in my study population, but female aggression was not influenced by either the presence a male neighbour or the number of males in the study area. In most species of pinniped, the attraction of multiple males can result in reproductive costs to the female, as the vicious male territorial fights have been known to displace females and injure pups (Doidge *et al.* 1984; Trillmich & Trillmich 1984; Harcourt 1991). Such effects can result in mother-pup separation and pup death by trauma; therefore, attraction of males to incite inter-male aggression should be selected against. Also, as males defend territories with well-defined boundaries, female aggression towards a male was not observed to attract investigation by neighbouring territorial males.

Past studies have suggested that the distribution of females may also be influenced by the presence of males, as females actively attempt to avoid male harassment (South American sea lion, Cappozzo *et al.* 2008). If this was the case, we would expect to see the presence of males influencing the location of the females in the rookery even after the mating season, as males were observed to harass females outside of this period. However, while the focal females' locations in relation to the sea and the nearest pool over the study period were significantly influenced by the number of males in the rookery, there was no significant relationship during the nursing period. This suggests that the focal females' site choice during the study period was most likely influenced by other factors such as the resources required for pup survival and thermoregulation, rather than an active avoidance of male harassment. The difference between the results of the sea lion study and this current study may be due to the inter-male interactions and inter-female interactions being significantly more detrimental to the females of the sea lions than in the fur seal, resulting from the female-raiding behaviour and higher frequency of male territorial fights in the South American sea lions (Campagna *et al.* 1988; Cassini 2000). Although this lack of influence of male presence during the nursing period could be attributed to the lower aggression and territorial behaviour of males in the post-mating period (Goldsworthy & Shaughnessy 1994), this is unlikely as the detrimental impact of the large-bodied males on the fitness of females would still be present.

Offspring defence

The focal females from this study showed significantly longer response and aggression distance towards female opponents in the presence of filial offspring compared to in the absence of offspring. This suggests that females are more responsive and less tolerant towards approaching adult females when their pup is present, and supports the theory that offspring defence is a function of female aggression in pinnipeds (Boness *et al.* 1982; Francis 1987; Cassini 2000, 2001; Fernández-Juricic & Cassini 2007). As done in the studies by Francis (1987), this study compared the behaviour of the same females in the presence and absence of their offspring, rather than comparing different individuals with or without pups, or comparing lactating or non-lactating females as was done in some past studies (e.g., Cassini 2001). This would have eliminated any bias arising from

individual variations in behaviour, age, size and differences in hormone levels between reproductive and non-reproductive females.
Pup defence against conspecifics as a function of female aggression has been suggested in a number of studies on various pinniped species (Christenson & Le Boeuf 1978). For example, the pups of female Northern elephant seals that showed higher frequency of aggression were observed to have experienced lower levels of attack from unrelated females (Christenson & Le Boeuf 1978). A study on grey seals proposed that female grey seals' aggression served to protect pups from other females, more likely to be aggressive to other females if her pup was between her and the approaching individual (Boness *et al.* 1982). The presence of filial offspring was found to increase the frequency of female aggression in both the northern fur seal and the California sea lion (Francis 1987). Cassini (2001) also found that females of the South American fur seals (*Arctocephalus australis*) whose pups were present showed increased levels of aggression towards other females compared to those of the females whose pups were absent (Cassini 2001).

Another explanation for the increased response and aggression distance of focal females in the presence of their pups is the response of the pup towards approaching conspecifics alerting their mothers earlier than if the female had been alone. This would have resulted in a higher level of detection or vigilance effect (Pulliam 1973), where the probability of spotting an approaching conspecific is increased with a greater group size. The contribution to vigilance from the pup was not supported by this study, as there were no differences in the response and aggression distance between the presence and absence of filial pups, towards approaching non-filial pups. Furthermore, increased vigilance would not be expected to be present early in the breeding season when the pup is young, during which period pups show very low levels of responsiveness towards approaching conspecifics.

Conspecific female aggression towards non-filial pups is one of the main causes of pup mortality in numerous species of pinnipeds. For example, in some species such as the northern fur seal and the South American fur seal, females were observed to fight over neonate pups which resulted in fatal injuries to the pup (Francis 1987; Harcourt 1992a). In Northern elephant seals, female aggression towards non-filial pups and female mob

attacks on lone pups cause mortality either directly via injuries or indirectly via mother-pup separation, and is the leading cause of pup deaths (Le Boeuf & Briggs 1977). Infanticide from conspecific aggression was also one of the two primary causes of pup mortality in the South American fur seal, along with starvation (Cassini & Fernández-Juricic 2003). In the Ohau Point population, females were also observed to attack pups without being approached or provoked, suggesting that female-pup aggression is prevalent. Although female aggression towards young is common in most pinnipeds (Maestripieri 1992), to my knowledge, pup mortality from female aggression has not been reported in the New Zealand fur seal. Only about 3 dead pups were observed in the study area, with causes of death unknown. Pup mortality in the New Zealand fur seal is mostly caused by starvation, and other reported causes include stillbirths, suffocation, drowning, trampling and predation (Mattlin 1978b). A past study conducted at the Ohau Point colony has also noted the observed low risk of female aggression causing injury to pups (Dowell 2005).

So why do female New Zealand fur seals show pup protection behaviour when the threat of female aggression to their pups' survival is relatively low? Although female aggression towards pups in New Zealand fur seals appears unlikely to induce fatal injuries, it may increase the likelihood of mother-pup separations as the pup moves away to avoid further attacks. As mother-pup vocal recognition is well developed in the New Zealand fur seal and pups are equipped to survive the female's foraging trips, short-term separations are unlikely to result in mortality through starvation. However, frequent and repeated separations caused by female aggression may result in reduced fitness of the pup as the pup expends more energy to move away from the aggressor which also results in interruptions in suckling bouts. Since New Zealand fur seal pups require the ability to fast between their mothers' feeding trips, being able to maximize nutrient intake before the next departure of their mothers would be critical for their survival between the feeding trips. The pups which are not able to consume the required amount for survival between the females' feeding trips due to interruptions from aggressive females would be fatally disadvantaged. In the New Zealand fur seal, starvation is the highest cause of pup mortality (Mattlin 1978b), and although milk-stealing from unrelated females is attempted, they are usually unsuccessful as females aggressively repel non-filial pups (Dowell 2005). Therefore, I theorise that the function of increased female aggression in the New Zealand fur seals in the presence of their

offspring is to reduce mother-pup separations induced by female aggression, rather than to reduce injury-related pup deaths. The lack of significant difference in female aggression between the birthing and nursing period, and over the study period also supports this theory. Many other female pinniped species have been shown to display higher frequency of aggression in the presence of their offspring just after parturition, compared to later in pup development (Harcourt 1992b; Phillips 2003). This is suggested to be caused by the females showing increased intensity of aggression when their pups are younger, and therefore, more vulnerable to attacks and injuries by unrelated females (Christenson & Le Boeuf 1978; Maestripieri 1992). For example, female South American fur seals were more likely to respond aggressively and to successfully repel approaching females postpartum (Harcourt 1992b). If the primary driver of aggression in the focal females in this study was prevention of injuries to offspring, we would expect to see a decline in inter-female aggression over the breeding and nursing season, as the pups grow larger and more able to defend themselves (Boness *et al.* 1982). If the female aggression acted to help maximise their pup's nutrient intake by reducing separations, it could be more critical to pup survival as the pup aged, as the duration of female foraging trips increase over the course of the breeding period. This can be supported by the evidence that pups can experience reduction in growth and increase in mortality rates as their mothers take longer foraging trips (Lea & Hindell 1997). Such effect could explain why the female's aggression distance and proportion of aggression towards females was not significantly lower during the nursing period, in comparison to the birthing period.

Female aggression is positively correlated to the probability of pup survival in the Northern elephant seals, as female aggression can successfully prevent or reduce mother-pup separations in this species (Christenson & Le Boeuf 1978). Mother-pup separations in elephant seals are usually fatal for the pup, due to their low physical mobility and poorly developed mother-pup vocal recognition. In contrast, otariids are highly mobile on land in comparison to phocids (Miller 1974), with their large pectoral flippers and hind-flippers that can be rotated forwards (Fish 1996; Hooker *et al.* 2005). The mother-pup recognition in otariids is also well developed, and pups experience extended mother-pup separations repeatedly during the females' feeding trips (McNab & Crawley 1975; Cawthorn 1985) during which the pups receive no maternal protection.

Thus, it has been suggested that otariid females' aggression as a function of pup protection would be less effective in comparison to phocids which remain on land until their pup weans, as otariid pups are vulnerable to attack by conspecifics during the females' foraging trips (Harcourt 1992b). A study on the South American fur seal found no differences in aggression between the females whose pups survived and whose pups did not survive (Harcourt 1992b). Therefore, we can deduce a similar relationship between female aggression and pup survival in other otariid species such as the New Zealand fur seal.

In most species which provide maternal care, female aggression also functions to protect young from predation (Lack 1968; Maestripieri 1992). For example, Uruguayan population of South American fur seal females were observed to defend pups against South American sea lions, despite the high risk to the female (Cassini 1998). In contrast, in the Peruvian population of the South American fur seal, females whose pups were being preyed upon by sea lions avoided direct confrontation (Harcourt 1992b), and this difference was attributed to the presence of both the Uruguayan fur seal and sea lion rookeries on the same island (Cassini 1998). New Zealand fur seals do not have natural terrestrial predators, though there have been observations of male New Zealand sea lions predating on New Zealand fur seal pups (Gentry 1987; Carey 1992; Bradshaw, Lalas & Mcconkey 1998). The instances of sea lion predation on fur seal pups are currently negligible, and as there are no sea lion rookeries near Ohau Point seal colony, female aggression as a function of pup defence against predators in terrestrial habitats is highly unlikely in the New Zealand fur seal.

Breeding site choice

Carey (1992) found that female New Zealand fur seals show higher levels of aggression in and around cooling substrates such as rock pools and shades. This study suggested that females are more likely to compete for areas high in thermoregulatory value to reduce the necessity of visiting the sea for thermoregulation, thereby increasing the lengths of pup attendance periods.

The distance of the focal females from the sea and rock pools in my study were observed to significantly decrease with an increase in rock temperature, which

indicates that female fur seals preferentially occupy the areas near the sea and the pools for thermoregulatory purposes. The lack of relationship between the time of day and the distance of the focal females from the sea and the pools suggests that the decrease with the rock temperature was not linked to the daily movement cycle (such as leaving and returning to the rookery from foraging) of the fur seal.

It was found that the distribution of females showed clustering around tidal pools, an important thermoregulatory resource, as the number of female neighbours was high in areas near the pools. However, although there was evidence of clustering in areas near the sea by neighbours of all demographics, the number of female neighbours was not significantly high near the sea. This may be due to the females preferentially occupying areas further from the sea during the birthing period. This finding suggests that pools are a sought-after resource for females, and supports the idea that the location of resources influence the distribution of females within the rookery (Cassini 2000). Although the distance and the proportion of aggression in the focal females during the entire study period were not influenced by the focal female's location, the proportion of aggression was found to be significantly higher in areas nearer to the sea and a pool within the birthing period. As the proportion of aggression was found to increase with increasing number of encounters, which in turn increases with the density of neighbours, the higher proportion of aggression near the sea and the pool could have been influenced by the increased rate of social interaction, rather than the presence of these thermoregulatory resources. However, the number of encounters was not significantly higher in these areas, eliminating the potential effect of increased neighbour density as a driver of increased aggression. As elevated aggression in certain sites likely indicates an increased effort of site defence, during the birthing period, the females occupying areas near these resources of higher cooling potential showed greater efforts to maintain their possession, as proposed by Carey (1992) .

The focal females were observed to be positioned significantly closer to the sea and a pool during the nursing season compared to the birthing season. As there were no significant differences in the rock temperature between these periods, this indicates that the females are likely to have sacrificed their thermoregulatory requirements to give birth in areas further from the thermoregulatory resources, to increase the

probability of pup survival. Areas near the sea present high risks of neonate being swept out to the sea, in which case pup will almost always drown (Mattlin 1978b) as neonates under the age of 10 days are unable to swim (McNab & Crawley 1975). The areas in the study area near the sea were flat, smooth rock surfaces, while areas more inland were formed of boulders and small rocks, which provide small pups with safe hiding spots from the direct sunlight and from being trampled by bulls (Crawley & Wilson 1976; Carey 1989). The abandonment of resting areas inland in preference for resting areas near the sea over the progression of the breeding season suggests that females prefer to rest and nurse near water, once their pups are able to swim and therefore able to safely utilize water as a thermoregulatory resource. A preference for areas near water was also observed in adult female Australian fur seals, as they were seen to move closer to the sea over the breeding season (Lourie *et al.* 2014).

The mean rock size of the focal female location was also seen to significantly differ between the birthing and the nursing period, with most of the females occupying areas on rocks smaller than 0.5 m in size during the birthing period while occupying areas on rocks larger than 0.5 m during the nursing period. This may also be an indication of females sacrificing their own site choice for the survival of their offspring. Females appear to select sites with small rocks on which to give birth on, which provide pups with small crevices in which they can seek shelter. Pups are the demographic the most vulnerable to heat stress (Lourie *et al.* 2014) and pup deaths can occur at high temperatures (Trites 1990; De Villiers & Roux 1992). Therefore, female New Zealand fur seals may experience reduced reproductive fitness by giving birth in low quality sites with no thermoregulatory resources suitable for neonates. Furthermore, the terrain which is primarily constituted of small rocks would also facilitate pup movement and therefore allow easier access to the mother for suckling. Giving birth or resting on a large rock could risk the neonate falling off the rock and receiving injury, or the pup being unable to climb up to suckle from the female. A group of large rocks also form deep crevices, into which neonates could fall. For example, a pup being born on a group of three large boulders (c. 1 m in diameter) was witnessed falling into a crevice in between, from which the pup could not escape on its own or with the mother's efforts to pull it out. Therefore, if pup survival is to be maximized, birthing site selection should include considerations for these environmental effects.

The significantly higher number of females observed close to the sea during the latter period of the study period could also be the result of a difference in the reproductive success in the females between the areas nearer to the sea and farther from the sea. The birthing location of a female can strongly influence the breeding success of a female (Parker *et al.* 2008), through the provision of higher quality resources to the offspring. The decline in the number of females with pups in the inland areas over the progression of the breeding season may have been caused by the breeding failure of these females, along with the thermoregulatory migration towards the sea. While females remain with their pup for approximately 8 days after birth, in high temperatures they may take short trips to a pool or the sea for thermoregulation, temporarily abandoning their pup. Females that give birth nearer to a pool or the sea would have an advantage over females more inland, as they are able to take shorter thermoregulatory trips; this would allow them to provide longer periods of maternal attendance (Carey 1992). Further research to explore the potential differences in the reproductive success within the rookery in regards to the birthing location would contribute important information to understanding the mechanisms of breeding site selection in this species.

Female spacing

The competition for space, and the resulting decline in female density has been proposed as a function of female aggression in many pinniped species, as high female density has been found to have strong correlations to reduced female reproductive fitness (Maestripieri 1992; Cassini 2000). The exhibition of territoriality to increase the rate of dispersal in reproductive females has also been suggested in other species, with the potential benefits of increased dispersal being reduced predation and constraints on the number of breeding individuals (Birds: Bergerud & Butler 1985). In pinnipeds, the defence of an area around the female is suggested to allow the protection of the pup from density-related effects and the use of the 'thermoregulatory resources' in the area by the mother-pup pair (Cassini 2000). If this was the case, we would expect the strength of female aggression to have an influence on the size of the 'female territory', and for the offspring of the more aggressive females to have higher chance of survival by experiencing lower density-related costs and gaining access to more

thermoregulatory resources. Additionally, if the size of female territory was to increase the pup's chances of survival, the mean approach-tolerance distance of focal females observed later in the season would be shorter, in comparison to the focal females observed earlier in the season, as the pups of the less tolerant females would have had a higher likelihood of survival. However, the strength of female aggression did not influence the size of the area around the focal female that successfully excluded opponents, and the aggression distance of focal females was not found to significantly differ between the birthing and the nursing periods. If the female aggression had evolved to regulate breeder population through actively preventing others from establishing pupping sites near them, significantly higher aggression distance and proportion of aggression would be expected during the female arrival and pupping periods; the aggression would also begin to taper off almost immediately after the pupping period as the last of the postpartum females depart on their feeding trips. However, no differences in the mean aggression distance and proportion were found between the pupping and nursing periods in my study population, suggesting that the positive relationship between the proportion of aggression and density is caused by an increase of inter-female competition for resources.

The nearest female neighbour distance did not differ between the birthing and the nursing periods, even though the number of females in the study area and the number of female neighbours were significantly lower during the nursing period. This suggests that the dispersion of females in the rookery is not mediated by the population density or the amount of available space, but rather, the individual distance maintained by all individuals.

Carrying capacity predictions and female dispersion

Unlike seabirds, female New Zealand fur seals are obligated to reproduce annually regardless of the population density of their natal or previous breeding site, as long as they are pregnant from the previous mating. Although aborted foetuses have been observed prior to the pupping season, no research has reported the ability to terminate pregnancy in response to environmental variables in pinnipeds to my knowledge. This results in the females returning to their natal or previous breeding colony, and potentially occupying new sites near the established colony if the colony is too densely

populated with other breeding females (Bradshaw *et al.* 2000; Boren *et al.* 2006). Such density-dependent emigration leads to expansion of colonies of high breeder density; to further understand the mechanisms of colony expansion, the current study used empirical data such as colony density and individual distance.

The size of the birthing zone was deduced from mapping the actual habitat used by pupping and lactating females during the birthing period of the study period; the area outside this was deemed 'unsuitable' for pupping, due to the lack of births and females nursing their pups in this area during the birthing period. It could be argued that this lack of births in the supposed 'non-birthing zone' was due to a low female density and the high quality (supposed 'birthing zone') habitats being occupied before the low quality areas. However, this is unlikely to be the case, as the Ohau Point seal colony is expanding northwards as well as towards the inland (Dangerfield 2015). The occurrence of expansion suggests that the Ohau Point seal colony, which includes the study area, is high in density and potentially close to the peak carrying capacity. The birthing zone also contains geographical features shared with other rookeries of the New Zealand fur seal, such as rocks smaller than boulders and less prominent slopes (Bradshaw *et al.* 1999), which provide pups with shelter and more forgiving terrain. The non-birthing sites were either large smooth rock formations exposed to the waves, or steep slopes formed of large boulders with deep crevices which new-born pups could fall into. Therefore, I propose that this distinct birthing zone provides resources necessary for pup survival, while the non-birthing zone does not, and that births are highly unlikely to occur in this area even with high population density.

The highest number of females counted at one time in the study area was 105 individuals (counted during the birthing period) indicating that the study area is able to provide enough space for at least 105 adult females at one time. However, this number would not be an accurate representation of the number of females that bred in this area during the 2014 – 2015 breeding season; this is due to the unknown rate of female turnover and the unknown number of non-parous (not pregnant) females in the area during the pupping season. As females arrive in the rookery to give birth 2 – 3 days before parturition (Miller 1975), and leave for their foraging trip approximately 8 – 9 days post-partum (Miller 1975; Crawley & Wilson 1976; Goldsworthy & Shaughnessy

1994), each female would be occupying space in the colony for a total of approximately 10 – 11 days. New Zealand fur seal females' first foraging trip usually lasts about 4 – 5 days, and the subsequent pup attendance period is about 2 – 3 days (Miller 1975). However, the females of the Ohau Point colony have been known to take shorter foraging trips, often as short as overnight, thought to be due to the Kaikoura canyon providing a rich source of prey at a geographically short distance of 2 km (Jaquet, Dawson & Slooten 2000; Boren 2005). Temporal variances between years in the length of foraging trips and foraging trips of less than 12 hours in duration during the summer has also been reported in the lactating New Zealand fur seal (Harcourt *et al.* 2002). After the first set of females have departed on their foraging trip, newly arriving females would be able to establish in their breeding sites; however, the occurrence of short foraging trips may result in the previous owners reclaiming their breeding sites, forcing the new arrivals to find new site. This would effectively minimize the rate of parous (pregnant) and postpartum (have given birth) female turnover on a number of breeding sites. The pupping period of the study population was estimated to be from 21st November to the 28th December from confirmed observations; thus, the initial period of reproductive females' pupping site occupancy could be calculated to begin approximately from the 18th November and end around the 6th of January, resulting in a total of 38 days of pupping, and 49 days during which the first parous female arrives and the last post-partum female departs for her first foraging trip. A similar length of pupping period of 42 days (18th Nov to 29th Dec) was reported for the New Zealand fur seal population of the Open Bay Islands (Miller 1975). Due to the initial period of site occupancy for pupping and mating (c. 10 – 11 days) being significantly shorter than the total birthing period (c. 45 days), and parous females arriving continuously through the breeding season (Miller 1975), it is likely that the turnover rate of parous females is not accurately represented by the highest female count of the birthing period. Additionally, the female population counts in this study would have included unknown numbers of non-parous adult females, as no effort was made to distinguish lactating females from non-lactating females in each female count. Since non-lactating females are not likely to have resided in the rookery for the entirety of the study period and may have had foraging cycles dissimilar to the lactating females due to the absence of reliant offspring (Arnould *et al.* 2001), their presence may have exaggerated the number of breeding females in the study area. Since non-lactating females would be expected to have had a

constant presence in the study area only during the mating season, their presence would have had the most significant influence on the total female count during this period.
Although the shape of females nipples have been examined and protruding state of the nipples along with the production of milk was assumed to be indicative of nursing pups (Harcourt *et al.* 2002), it has not been confirmed if all nursing females show such visually examinable characteristic. Visually notable differences in the nipples of different individuals were observed, but whether or not these were indicative of reproductive condition was not further investigated as it was outside the scope of this study. Further research to explore the methods of visually assessing the reproductive state of females would be helpful in understanding the ratio of non-breeding females, and the influence of their presence on the density-dependent spatial population dynamics.

This led me to use pup count of the study area, instead of the direct count of females. Pup count is commonly used as a method of estimating population sizes in otariids, as an accurate count of adults is made highly difficult due to their foraging cycles, resulting in an unknown number of animals absent from the rookery at any one time (Stirling 1971; Wickens & Shelton 1992; Bradshaw *et al.* 2000). Pups also constantly remain in their natal rookery until weaning, and are easily distinguished by their dark pelage and small size (Wickens & Shelton 1992). As the number of pups in the study area at the end of the birthing period would almost directly correlate to the number of females that gave birth (the occurrence of stillbirths may result in underestimation), pup count was used as a more reliable estimation of the number of parous females that has occupied a site in the study area. There is limited amount of data on the neonate mortality of New Zealand fur seals, therefore the number of pups born (alive or dead) cannot be estimated but it can be assumed to be higher than the actual count.

The study area carrying capacity prediction data using the nearest female neighbour distance shows that the predicted carrying capacity of the study area is 195.33 females. However, this does not necessarily take into account all the required space between females to allow the movement of individuals to and from the sea, as a number of the nearest neighbour distance was as short as 0.25 m (0.6% of 346 neighbours of all focal

females); evidently insufficient to allow adult females to pass through. Thus, the use of the nearest-neighbour distance may have biased the individual space to be smaller. Therefore, it may be a better method to measure the amount of individual space around the perimeter of the female by taking the mean of the distances of all direct-neighbours (individuals directly neighbouring the focal female, with no other individuals positioned between them and the focal female), rather than using the nearest-neighbour distance. The nearest-neighbour distance would be a reliable method of carrying capacity prediction in the studies of colonial seabirds, which access their breeding sites from the air. Conversely, if the female fur seals' breeding sites were so tightly packed, it would be incredibly difficult for newly arriving females to access the deeper parts of the rookery, which would effectively prevent some areas from being occupied. This can be supported by the observations from this study; females with resting sites near the cliff were observed to be unable to approach the main pool or the sea without inciting aggression from females resting or nursing around the seaward edge of the study area. By taking into account the distance from all neighbouring females directly around the focal female, the amount of space which were present to allow the female movement to and from the sea or the pools would be included. Future research assessing this total-direct-neighbour distance and its comparison with the nearest-neighbour distance method would be beneficial in further understanding the methods of population and carrying capacity prediction of non-avian breeding colonies.

The type of substrate would also negatively influence the number of seals an area would be able to hold at any one time, as heterogeneous substrate such as boulders would result in the distance between individuals being longer. In contrast, terrain with cavities large enough for adult females may have a positive influence on the carrying capacity of the habitat in relation to area size, as it would allow overlaps of individual areas. The considerable difference between the breeding female carrying capacity predictions obtained using the birthing zone and the nursing zone shows that not accounting for the differences in habitat-use between the birthing and nursing periods can result in a gross overestimation of the carrying capacity. This stresses the importance of analysing the mechanisms of breeding site selection and identifying the areas used for reproduction.

In the Ohau Point seal colony, there was no significant relationship between aggression and the degree of female dispersion, as the distance of the nearest established female neighbours from the focal female were not significantly influenced by the level of aggression from the focal female. This suggests that females establishing a resting site or a nursing site near the focal females were unaffected by the strength of aggression from the focal females. The mean aggression distance (0.45 m) was also significantly shorter than the mean nearest female neighbour distance (0.76 m). This suggests that the inter-female spacing is not primarily mediated by the aggression distance of resident females, but rather by the individual distance, where both the resident and the newly establishing females attempt to maintain a certain distance. If the inter-female spacing was mediated solely by female aggression, we would expect the mean nearest female neighbour distance to be similar to the mean aggression distance during periods of high density. As there was a significant disparity between the predicted carrying capacity using the aggression distance (303.55 individuals) and the nearest-female neighbour distance (195.33 individuals), the need for a detailed analysis of the relationships between the response variable and the predictor is emphasized. If the aggression distance, initially assumed to be the mediator of female dispersion, was used for the prediction of the carrying capacity without the analyses of its effects, a significant overestimation would have occurred.

The predicted carrying capacity of the study area using the nearest-female neighbour distance was 195.33 individuals, while the estimated number of females which gave birth in this area was 102 individuals. This implies that the study area is only at half of its breeding female carrying capacity. However, the Ohau Point colony was confirmed to be expanding as of the breeding season during which this research took place (2014-15), as females were observed to be pupping on the rocky coastal area directly north of the Ohau Point stream carpark (personal observation), where no pupping was observed until recently. The Ohau Point seal colony has been rapidly increasing since the 1990s, and 32% annual increase in pup productivity was reported for the period from 1990 to 2006 (Boren *et al.* 2006). As of the 2015 – 16 breeding season, territory establishment by males and pupping were also reported to be occurring up the Ohau Point stream, which appears highly unusual as the New Zealand fur seal's habitat usually consists of rocky coastal areas (Miller 1974; Crawley & Wilson 1976; Bradshaw *et al.* 1999; Dickie & Dawson 2003). The establishment of females at the edge of the colony and in unusual

habitat suggests that the colony is near its maximum carrying capacity. A number of reasons may help explain the large disparity between the predicted carrying capacity and estimated number of females in the area.

Firstly, as already mentioned, the presence of non-parous females in the rookery during the birthing and mating period may have resulted in a lower number of parous females than would be expected. The presence of non-breeders is known to be able to have a detrimental influence on the reproductive performance of a population (López-Sepulcre & Kokko 2005). Although the non-parous females are likely to have occupied zones within the study area different to the parous females, they still may have competed for the areas high in thermoregulatory value such as areas near the pool. By contributing to the competition for breeding sites, non-parous females may have effectively prevented some parous females from establishing, decreasing the net productivity of the area which would have been reflected in the pup count.

Secondly, the pup count may have missed an unknown number of individuals. Visual count of pups is unlikely to be highly accurate, especially for many species of fur seals which primarily breed on rocky, heterogeneous terrain, and as pups have a tendency to hide under rocks for safety and thermoregulation (Stirling 1971). Such effect could be seen in the pup counts performed in this study, as pup counts varied greatly between each sampling times; for example, on the last day of the birthing period, the pup count for each sampling times were 93, 68 and 97, respectively. As the majority of pups were not mobile enough to move long distances to neighbouring subsets of the colony, and the first swimming pups were also seen on this day (2 individuals); this suggests that the low count during the mid-day can only be attributed to the pups being hidden under rocks. This demonstrates that nearly 44% of total pups (highest pup count during birthing period was 102) were able to effectively be hidden from view, greatly influencing the accuracy of pup number estimations.

Thirdly, the study area may not be providing sufficient thermoregulatory resources to support all resident females if all the available sites within the birthing zone were to be occupied. During high tide, the study area has one large (c. 12 m in length, 4.4 m in width) pool, and a system of smaller and shallower pools. The area has boulders and rock formations (largest c. 2.5 m in height), but none can sufficiently provide shade during most of daylight hours and there are no caves. As Carey (1991) found the number of females to significantly increase with the amount of shaded area available,

the lack of shade in the Ohau Point study area may be limiting the potential occupancy of some sites.

Lastly, as mentioned, the use of the nearest-female neighbour distance method to calculate the dispersion of females may have resulted in a smaller area size. I expect that the use of the total-direct-neighbour distance to improve the accuracy of the estimation of female dispersion by including the between-individual space for female movement.

This assessment of the carrying capacity of the study area using the female dispersion measurements demonstrates the complexity of predicting the breeding population size in terrestrially-breeding mammals with individual variations in parturition dates and inconsistent space occupancy. Although the results of this prediction contributes to a further understanding of the effects of time and habitat occupancy on the dispersion of females in the New Zealand fur seal, for a more reliable prediction of the expansion and direction of the colony, additional elements such as the space for movement between settled individuals, the influence of the number of non-breeders and the suitability of potential habitats around the existing colony need to be taken into consideration.

Implications

Human-induced climate change has been shown to cause significant changes in the habitat ranges of various species, through an increase in global temperature (Walther *et al.* 2002; Chen *et al.* 2011). As the behaviour and within-rookery distribution of female New Zealand fur seals were found to be influenced by temperature in this study, it is likely that global temperature change will alter the intra-species interactions and distribution of this species. For example, increase in temperature may result in higher clustering around high quality thermoregulatory resources such as pools, and also result in a decreased reproductive success of sites that are further from this resource as increased thermoregulatory trips reduce the period of maternal attendance. Such effect would result in a progressive reduction in the size of breeding habitats centered around thermoregulatory resources with increasing temperature, decreasing the carrying capacity of a given habitat area. Therefore, a failure to account for the species' spatial response to environmental influences such as temperature in a period of ongoing climate change may result in an overestimation of the carrying capacity, leading to an earlier expansion of the colony than would have been predicted.

The methods used in this research would be applicable in future studies of intra-specific aggression and spatial dynamics of other species of fur seals, as well as other colonially-breeding terrestrial species.

Research limitations

Kin recognition

A potential bias in the results may have arisen from philopatry (return to their natal site) and site fidelity (return to a non-natal site) in New Zealand fur seals (Gentry 1998). Philopatry and site fidelity in this species has been suggested to be high (Stirling 1971; Bradshaw *et al.* 2000), and philopatry in the Ohau Point population has also been observed (L. J. Boren, personal communication, 2016). Many otariids return to the site of their birth to breed as they reach their reproductive age, and in some seals there also is evidence of small-scale philopatry and site fidelity, where they either return to their natal area or past breeding area within a rookery for reproduction (Gentry 1998; Bradshaw *et al.* 2000; Wolf & Trillmich 2007). Such small-scale behaviour is likely to result in neighbouring breeding females to be related or familiar, which may decrease the degree of aggressiveness towards one another and their offspring (Baldi *et al.* 1996; Wolf & Trillmich 2007; Clutton-Brock & Lukas 2012). Grey seal females have been found to preferentially select breeding sites near their mothers (Pomeroy, Twiss & Redman 2000), which could additionally increase the degree of relatedness between females breeding in close proximity. Due to the highly developed mother-pup recognition in the New Zealand fur seal (Dowell 2005), and the longer nursing duration compared to the grey seal (Grey seal: c. 2.5 weeks, Boness & James 1979; NZ fur seal: c. 10 months, Ryan *et al.* 1997; Harcourt 2001), it cannot be dismissed that kin recognition and preference behaviour may also have influenced the nearest female neighbour distance results. Male grey seals have also been shown to display reduced rates of aggression, in presence of familiar neighbours (Bishop, Pomeroy & Twiss 2015); if such effect occurs in the female New Zealand fur seals, older females who are familiar with

their neighbours from previous breeding seasons may show less aggression in comparison to young females or emigrants.

The degree of relatedness between females was not assessed as this was beyond the scope of the study. Capturing two or more neighbouring females at one time would also have been significantly difficult, as females are highly wary of humans and readily retreat to the sea with rookery disturbance (Barton *et al.* 1998; Boren *et al.* 2002). As there has been no study focused on the small-scale philopatry of females in this area, we were unable to analyse and control for the degree of familiarity between the females that pupped or rested in close proximity to one another.

Individual variation

It was not possible to confirm the selection of different female individuals for observation, as most females (89%) in the study area were not identifiable by physical markings (scars, coat irregularity) or tags at any time during the study period. As 184 observation samples were obtained, and the estimated number of postpartum females in the study area was 102 individuals inferred from the pup count, at least nearly half of the observations made could have been on a female that was observed already. Although an effort was made to minimize observation of same individuals by selecting mother-pup pairs at different sites within the colony, incidental use of same individuals as focal animals inevitably occurred due to the sample size being larger than the population of focal animals, which may have led to biased results if individual variation in aggressive behaviour was present in this population. A study of the Antarctic fur seals by Meise *et al.* (2016) found that pups born from females who were residents of high density colony showed higher levels of testosterone, the hormone which mediates aggression, which suggests that the aggressiveness of Antarctic fur seals may vary according to the density of their natal colonies. Future research to investigate the measurement and comparisons in the degree of individual variations in aggression would be valuable in understanding the effects of such variation on multiple population processes. The females which were visually identifiable were either only able to be distinguished for a certain period of time, left the study area, had their distinguishing features hidden from sight or lost, or their periods of return to the study area did not overlap with the periods of my study area visits; this is because sighting of the distinguishable individuals were highly staggered, and only 27% (3 of 11) were sighted

after the 10th of February. The lack of continued sighting for the 73% of the initially distinguishable individuals is highly likely to be attributed to moulting. This is because the 3 individuals that were repeatedly sighted until the last month of the study period were all identifiable by tags, while the distinguishing features of the rest of the group were either markings on their coat, or their pups (one tagged, one with unique coat, both of which could be lost or altered through moulting). Future research investigating the potential methods of identifying unmarked otariid females, which usually have plain, uniformly coloured pelage, using physical characteristics such as the shape of fore-flippers would contribute significantly to the studies of pinniped behaviour.

Direction of approach

The direction at which the opponents approached the focal female may have influenced the response and aggression distance of the focal female. Such effect could have occurred if the female was unaware of individuals approaching due to being out of sight (e.g., behind the female); this would result in a shorter response and aggression distance. Although the direction of approaching seals was noted, I was unable to analyse this data due to time constraints.

The level of awareness of the focal female, and the varying levels of awareness between the different times of day may have resulted in lower mean of the response and aggression distances. Although the 'level of awareness' of the focal females towards approaching seals has been taken into account and excluded in the analyses of female aggression in a past study on the grey seal (Boness *et al.* 1982), it was not taken into account in the current study and all instances where there may have been a degree of 'unawareness' on the focal females' part were included in the analyses. This is because 'awareness' in animals is difficult to measure and prove, and it cannot be said for certain if the animal was actually unaware, or chose not to respond to the opponent. Seals have well developed olfactory and auditory senses, which are used as the primary mechanisms of communication and individual recognition (Phillips 1999; Charrier *et al.* 2003; Insley, Phillips & Charrier 2003). Therefore, a visual assessment of the degree of 'awareness' in these animals in relation to human behaviour and senses is unlikely to be a reliable method of measurement.

Repeated interactions

There were a number of instances in which the same individuals were involved in multiple interactions with the focal female within a single observation period. A set of repeated agonistic interactions with the same individual may have influenced the response and aggression distance, as well as the proportion and intensity of aggression, as the focal female would have been increasingly vigilant of the opponent, and potentially increasingly aggressive due to the repeated offending.

The results from this research provide important information on the function of aggression and the dispersion of female New Zealand fur seals within a subset area of the Ohau Point seal colony. Female aggression was observed to be influenced by a range of environmental and biotic factors, such as the time, temperature, number of neighbours, location of the females and the presence of a filial pup. The results from this study will provide assistance in further investigations of the function of aggression in female pinnipeds and the spatio-temporal changes in the distribution of females within a rookery. The predictions of the breeding female carrying capacity of a subset of a New Zealand fur seal colony made using the 'nearest neighbour distance' provide valuable information outlining the importance of investigating the spatio-temporal changes in female breeding site choice for the estimation of the carrying capacity and expansion of colonies. In light of these results, I propose that a novel method of measuring dispersion by using the distance between all direct neighbours and the focal female (total-direct-neighbour distance) would be a more appropriate method in investigating the dispersion of female otariids.

Conclusion

The objective of this research was to investigate the functions of the conspecific aggression behaviour of female New Zealand fur seals and its influences on the spatial rookery dynamics. Aggression towards conspecifics is commonly displayed by the females of many pinniped species; however, it has not been studied as extensively as male aggression due to its lower intensity and ambiguity of its benefits. Social behaviour, such as aggression, in colonially breeding species can assert a considerable influence on the population dynamics of the colony from the collective sum of inter-individual interactions.

Through the application of the measurements of aggression largely unused in previous studies of pinnipeds, this research provided an outline of the functions of aggression in the female New Zealand fur seals and demonstrated that the functions of aggression can be influenced by the unique social behaviour and reproductive ecology of each species. By using these results in conjunction with the nearest-neighbour distance measurements, this research was also able to evaluate the influence of the inter-female aggression on the rookery dynamics of the New Zealand fur seal to a certain extent. During this research various avenues of further research were identified, such as the suggested use of total-direct-neighbour distance, impact of non-breeders on female dispersion, the degree of small-scale philopatry and site fidelity, and the influence of kin recognition on the inter-female aggression of the New Zealand fur seal. These would deliver imperative information in a reliable prediction of the expansion of seal rookeries, and will be of significant contribution to the current knowledge of the mechanisms of population dynamics of pinnipeds.

Research findings

The analyses of female aggression in the New Zealand fur seal using a combination of various measures of aggression allowed an investigation into the function of aggression from novel angles. I found that the inter- female aggression in New Zealand fur seals

was driven by a combination of various functions, such as thermoregulation, offspring defence and resource defence.

Through the measurement and analyses of the aggression distance, previously unused in studies of pinniped females, I demonstrated the degree of influence that the environment can assert on the social behaviour of this species. I found that higher temperature caused shorter agonistic interaction distances in females; as aggression between colonial individuals can promote emigration and prevent immigration, temperature is likely to have a substantial influence on the spatial population dynamics in New Zealand fur seal rookeries. In accordance with many previous works on the conspecific aggression in pinnipeds, I found that the female New Zealand fur seals displayed increased aggression in higher densities. In contrast to a number of previous studies (e.g., Campagna *et al.* 1992; Cassini & Fernández-Juricic 2003), females of the New Zealand fur seal were not found to group in higher densities in the presence of dominant males, or increase their aggression as a result of the greater degree of grouping. This disparity was attributed to the low risk of female mortality arising from interactions with males in this species, and demonstrates that variances in inter-sexual interactions can result in variances in inter-species behaviour. I showed that aggression functioned to protect offspring from female conspecifics, a common driver of female aggression in many pinnipeds, owing to a high prevalence of female-pup aggression. However, due to the consistency in female aggression over the progression of the breeding period and the very low pup mortality attributed to conspecific aggression in the New Zealand fur seals, I proposed that instead of serving to minimize direct mortality from conspecific attacks, female aggression in presence of her offspring primarily functioned to minimize interruptions to the pup's suckling bouts. Through the use of focal female locations' distance to thermoregulatory resources such as the sea and pools, I showed that females expend more effort to defend breeding or resting sites of higher perceived quality as previously proposed by Carey (1992), and that the perceived quality of sites to lactating females differ between the birthing and the nursing period. During the birthing season, the focal females were found to be occupying areas further from the sea and the pools than during the nursing season, thereby sacrificing their thermoregulatory requirements to a certain extent to increase the survival rate of their offspring. Also, through an analysis of the rock size of the focal

female locations, it was shown that female site choice was also influenced by substrate, as females preferentially occupied areas of substrate type that maximized their pups' survival. Therefore, through an investigation of the functions of aggression in the female New Zealand fur seals which was previously largely unexplored, it was shown how the influence of differences in the breeding ecology, physiology and social interactions can result in considerable variations in behaviour between species.

By the mapping of the occupied sites within the study area for each of the birthing and the nursing period, I found evidence of spatio-temporal changes in within-rookery female site occupancy in the New Zealand fur seal. In contrast to my original hypothesis, aggression distance was not the primary mediator of female territory size and the resulting degree of dispersion, as it had no influence on the focal females' distance from neighbouring females or the number of neighbouring females. Therefore, I concluded that nearest-neighbour distance was more likely to be a more reliable measurement of female dispersion, as it directly measures the area around the female that successfully prevented the establishment of individuals. However, in analysing the results of the prediction of the carrying capacity of the area using the nearest-female neighbour distance method, I reached a conclusion that this method of measuring female dispersion was not sufficiently appropriate for use in exploring the individual dispersion in otariids. This was due to the fact that the nearest-female method was likely to have represented only the minimum individual space of the female, by not taking into account the space required in between established individuals for female movement to and from their thermoregulatory and foraging movements. Therefore, a new method of measuring female dispersion in otariids was suggested, where the distances from all females directly neighbouring the focal female are measured. I also demonstrated that an assessment of site use between different periods within the breeding season is imperative for more reliable predictions of female dispersion and carrying capacity, by showing the considerable differences in the breeding site choice of the females between the areas used in the birthing and nursing periods.

Through the assessment of the effects of female dispersion on spatial population dynamics of the New Zealand fur seal, I found that the measurement of the degree of dispersion in pinnipeds is more complex than initially expected, as the breeding sites are not fixed in location and space for mobility is required in between occupied sites.

Therefore, a further investigation and testing of methods of measuring the female dispersion, such as the total-direct-neighbour distance, would make a significant contribution to future studies in the spatial population dynamics of group-breeding species. I also propose that to be able to make reliable predictions of colony expansion in the New Zealand fur seal, further studies are required in regards to philopatry, site fidelity, kin recognition and the turnover rate of females during the birthing season.

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Appendix

Table 1. The effects of environmental predictors on the frequency of focal female responses towards approaching conspecifics. Nonparametric regression and Kruskal-Wallis tests were used.

Response frequency			
Predictor	n	Bandwidth	p
Rock temperature	172	121415785	**0.003**
Tide level	184	15109880	0.238
Wind speed	177	1.665583	0.581
Wave height	176	6941326	0.155
Percentage of cloud cover	175	22.19087	0.356
Time of day	184	H(2): 10.056	**0.006**

Table 2. The effects of environmental predictors on the focal female response distance. Multiple linear regression and ANOVA were used.

Response distance			
Predictor	n	t	p
Rock temperature	154	-2.1	**0.037**
Tide level	164	-1.53	0.127
Wind speed	159	$F_{4,154}$= 0.408	0.803
Wave height	158	$F_{4,153}$= 1.113	0.353
Percentage of cloud cover	157	1.22	0.224
Time of day	164	$F_{2,161}$= 2.26	0.108

Table 3. The effects of environmental predictors on the focal female aggression distance. Multiple linear regression and ANOVA were used.

Aggression distance			
Predictor	n	t	p
Rock temperature	154	-2.003	**0.047**
Tide level	165	-1.145	0.25
Wind speed	159	$F_{4,154}$= 1.779	0.136
Wave height	158	$F_{4.154}$= 1.785	0.135
Percentage of cloud cover	157	1.04	0.3
Time of day	165	$F_{2,162}$= 0.234	0.791

Table 4. The effects of environmental predictors on the proportion of focal female aggression. Nonparametric regression and Kruskal-Wallis test were used.

Proportion of Aggression			
Predictor	n	Bandwidth	p
Rock temperature	165	14215691	**0.033**
Tide level	176	0.800255	0.579
Wind speed	169	H(4)= 6.799	0.147
Wave height	168	H(3)= 5.462	0.141
Percentage of cloud cover	167	21.19947	**0.042**
Time of day	176	H(2)= 12.366	**0.002**

Table 5. The effects of proportion of female aggression, study area population and number of neighbours of focal female on focal female response frequency. Nonparametric regression was used.

Response frequency			
Predictor	n	Bandwidth	p
Proportion of aggression	176	0.3183519	0.08
Study area population	184	21.88052	**0.0003**
Number of neighbours	184	5956578	**<0.0001**

Table 6. The effects of biotic predictors on focal female response distance. Multiple linear regression was used.

Response distance			
Predictor	n	t	p
Number of encounters	164	0.806	0.421
Proportion of aggression	155	-2.479	**0.014**
Study area population	164	-0.409	0.683
Number of neighbours	154	-1.424	0.156

Table 7. The effects of biotic predictors on the focal female aggression distance. Multiple linear regression was used.

Aggression distance			
Predictor	n	t	p
Number of encounters	165	-1.323	0.187
Proportion of aggression	165	0.623	0.534
Study area population	165	-0.371	0.711
Number of neighbours	165	-1.568	0.119

Table 8. The effects of biotic predictors on proportion of focal female aggression. Nonparametric regression was used.

Proportion of aggression			
Predictor	n	Bandwidth	p
Number of encounters	176	8.076742	**0.03**
Study area population	176	117465401877	0.55
Study area female population	176	238150170470	0.674
Number of neighbours	176	4447245582	0.193
Number of female neighbours	176	13165653	**0.02**

Table 9. The effects of focal female aggression distance on the mean distance and number of each neighbour demographic. Nonparametric regression and simple linear regression were used.

Aggression distance			
Response variable	n	Bandwidth	p
Distance from male neighbours	19	1976811	0.303
Distance from female neighbours	133	0.3823627	0.411
Distance from pup neighbours	124	t= 0.054	0.957
Aggression distance			
Response variable	n	Bandwidth	p
Number of male neighbours	165	4421207	0.306
Number of female neighbours	165	1366539	0.306
Number of pup neighbours	165	682698.9	**0.002**

Table 10. The effects of proportion of focal female regression on the mean distance and number of each neighbour demographic. Nonparametric regression and simple linear regression were used.

Proportion of aggression			
Response variable	n	Bandwidth	p
Distance from male neighbours	22	0.1977621	**0.028**
Distance from female neighbours	142	5402103	0.178
Distance from pup neighbours	128	t= 1.273	0.205
Proportion of aggression			
Response variable	n	Bandwidth	p
Number of male neighbours	176	0.09397727	0.105
Number of female neighbours	176	0.1180071	**0.032**
Number of pup neighbours	176	2572985	0.551

Table 11. The effects of distance of focal female from male neighbours and number of female neighbours on proportion of focal female aggression. Nonparametric regression was used.

Proportion of aggression			
Predictors	n	Bandwidth	p
Distance from male neighbours	22	7039453	0.411
Number of female neighbours	176	4529969	**0.035**

Table 12. The effect of time of day on focal female locations' distance from the sea and the nearest pool. ANOVA and Kruskal-Wallis tests were used.

Distance from the sea			
Predictor	n	F/H	p
Time of day	114	F= 0.609	0.437
Distance from the nearest pool			
Predictor	n	R2	p
Time of day	114	H(2)= 5.02	0.081

Table 13. The effects of the focal female locations' distance from the sea, nearest pool, size of rocks on number of neighbours and number of female neighbours of focal females. Nonparametric regression and Kruskal-Wallis tests were used.

Number of neighbours			
Predictor	n	Bandwidth	p
Distance from the sea	131	11.129	**0.02**
Distance from the nearest pool	131	24339572	**0.03**
Rock size	128	H(2): 19.139	**0.0007**
Number of female neighbours			
Predictor	n	Bandwidth	p
Distance from the sea	131	90781309	0.055
Distance from the nearest pool	131	245019066	**0.015**
Rock size	128	H(4): 11.726	**0.02**

Table 14. The effects of the focal female locations' distance from the sea, nearest pool, size of rocks on focal female response distance, aggression distance and proportion of aggression. Nonparametric regression, ANOVA and Kruskal-Wallis were used.

Response distance			
Predictor	n	t	p
Distance from the sea	113	-1.784	0.077
Distance from the nearest pool	113	1.568	0.119
Rock size	111	$F_{4,106}$=1.241	0.298
Aggression distance			
Predictor	n	t	p
Distance from the sea	114	-0.113	0.91
Distance from the nearest pool	114	-0.232	0.82
Rock size	112	$F_{4,107}$=1.843	0.126
Proportion of aggression			
Predictor	n	Bandwidth	p
Distance from the sea	114	43391347	0.083
Distance from the nearest pool	114	0.9319516	0.236
Rock size	112	H(4)= 2.045	0.728

Table 15. The effects of the focal female locations' distance from the sea and nearest pool on focal female response distance, aggression distance, proportion of aggression and number of encounters during birthing period. Simple linear regression and nonparametric regression were used.

Response distance during birthing period			
Predictor	n	t	p
Distance from the sea	22	0.108	0.916
Distance from the nearest pool	22	0.074	0.942
Aggression distance during birthing period			
Predictor	n	t	p
Distance from the sea	19	-0.392	0.7
Distance from the nearest pool	19	-0.421	0.679
Proportion of aggression during birthing period			
Predictor	n	Bandwidth	p
Distance from the sea	22	104709980	**<0.0001**
Distance from the nearest pool	22	163066350	**0.018**
Number of encounters during birthing period			
Predictor	n	Bandwidth	p
Distance from the sea	24	45440081	0.471
Distance from the nearest pool	24	164481077	0.058

Table 16. The effects of the focal female locations' distance from the sea and nearest pool on focal female response distance, aggression distance and proportion of aggression during nursing period.

Response distance during nursing period			
Predictor	n	Bandwidth	p
Distance from the sea	102	14.86723	0.78
Distance from the nearest pool	102	34494831	0.699
Aggression distance during nursing period			
Predictor	n	Bandwidth	p
Distance from the sea	95	29.10738	0.639
Distance from the nearest pool	95	31783598	0.717
Proportion of aggression during nursing period			
Predictor	n	Bandwidth	p
Distance from the sea	102	9275137	0.491
Distance from the nearest pool	0.2	9.661554	0.386

Table 17. Effect of number of males during the study period and number of males during the nursing period on the focal female location. Simple linear regression (distance from the sea), nonparametric regression (distance from the nearest pool) and ordinal logistic regression (rock size) were used.

Number of males			
Response variables	n	t	p
Distance from the sea	131	2.578	**0.011**
Distance from the nearest pool	131	Bandwidth: 1.205	0.421
Rock size	128	-4.408	**<0.0001**
Number of males during the nursing period			
Response variables	n	t	p
Distance from the sea	107	0.451	0.653
Distance from the nearest pool	107	Bandwidth: 1.229	0.584
Rock size	104	0.071	0.943

Table 18. The effect of the environmental and biotic predictors on nearest female neighbour distance from focal female. Ordinal logistic regression and Kruskal-Wallis test were used.

Nearest female neighbour distance			
Environmental Predictors	n	t	p
Rock temperature	136	-2.114	**0.035**
Tide level	146	1.225	0.22
Wind speed	139	H(2)5.6456	0.227
Wave height	138	H(2)2.0543	0.726
Percentage of cloud cover	138	0.927	0.354
Time of day	146	H(2)10.0651	**0.007**
Biotic Predictors	n	t	p
Study area population	146	-1.443	0.149
Number of neighbours	146	-2.681	**0.007**
Proportion of aggression	143	-1.634	0.102
Study area female population	146	-0.824	0.41
Number of female neighbours	146	-5.681	**<0.0001**
Response distance	143	2.342	**0.019**
Aggression distance	134	-1.539	0.124

Table 19. Effect of focal female locations' distance to the sea, nearest pool and size of rock on nearest-female neighbour distance of focal females.

Nearest female neighbour distance			
Predictors	n	t	p
Distance to the sea	101	-1.484	0.138
Distance to the nearest pool	101	2.379	**0.017**
Rock size	98	0.771	0.441

Table 20. Prediction of the study area carrying capacity of breeding females for birthing period and nursing period, in reference to each periods' size of site occupancy zone . Two methods of estimating female dispersion (aggression distance and nearest neighbour distance) were used to compare the difference between these methods.

	Birthing period (area size 475m^2)	Nursing period (area size 1155.46m^2)
Prediction using mean aggression distance	303.55	750.79
Prediction using mean nearest neighbour distance	195.33	428
Actual female count (average)	74	37.8
Actual female count (highest)	105	80
Actual pup count (highest)	102	149